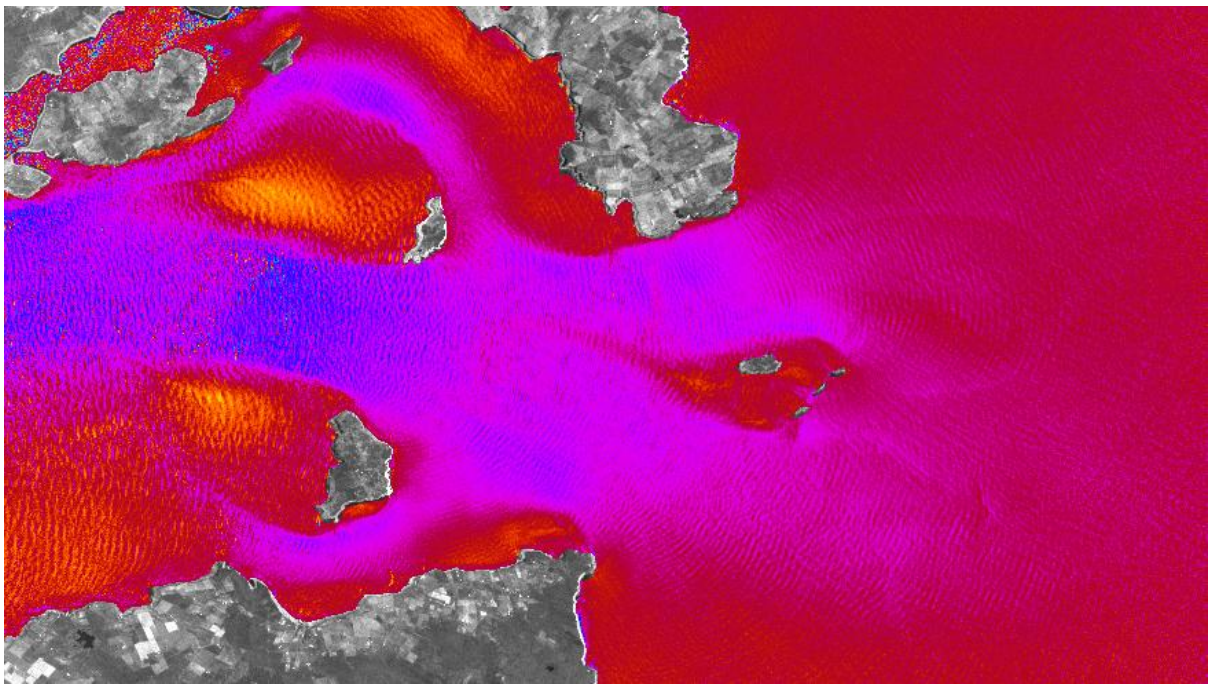
Guerin AJ, Jackson AC, Bowyer PA, Youngson AF. *Hydrodynamic models to understand salmon migration in Scotland*. London: The Crown Estate, 2014. Marine Research Report.

THE CROWN ESTATE

Marine Research Report

Hydrodynamic models to understand salmon migration in Scotland

Hydrodynamic models to understand salmon migration in Scotland



Andrew J. Guerin, Angus C. Jackson, Peter A. Bowyer and Alan F. Youngson

ISBN: 978-1-906410-52-0

Published by The Crown Estate.

This report is available on The Crown Estate website at: www.thecrownestate.co.uk

Suggested Citation
Guerin, A.J., Jackson, A.C., Bowyer, P.A. and Youngson, A.F. 2014. 'Hydrodynamic models to understand salmon migration in Scotland.' The Crown Estate, 116 pages. ISBN: 978-1-906410-52-0.

Title page image
A radar interferogram of the turbulent waters moving through the Pentland Firth, which links the Atlantic Ocean and the North Sea. The false-colour image is constructed from differences between two radar images taken by the sensitive, paired camera systems on board the TanDEM-X and TerraSAR-X satellites. In this case, water is flowing from east to west (an ebb tide). Slow moving water is shown as dark red to orange and the fastest water, which is coloured blue, is moving at about 3 $m.s^{-1}$ away from the line of vision of the radar systems. In situ measurements of water velocity can exceed 7.5 $m.s^{-1}$. These extremely rapid velocities are caused by tidal currents being forced through the bottleneck formed by this narrow strait. The Pentland Firth is potentially one of the main routes taken by migrating Atlantic salmon. This image illustrates some of the hydrodynamic challenges faced by these fish and underlines the importance of reliable information about how salmon deal with or avoid these conditions.

Executive Summary

Scotland has set the goal of producing the equivalent of 100% of its electricity demand from renewables by 2020; this will involve so-called 'marine renewables' – offshore wind, wave and tidal power. Since these technologies are still under development, the potential environmental implications of their deployment are unclear.

The Atlantic salmon (*Salmo salar*) is a migratory species of significant conservation and socio-economic importance around the coasts of Scotland, and in many Scottish rivers. Improving our understanding of the biology and migratory behaviour of these iconic and economically valuable fish is particularly important because of apparent long-term population declines and the possibility that migrating salmon may pass through, or close to, marine renewable energy development sites.

This report is concerned with methods for assessing the likelihood that salmon originating from Scottish rivers will pass close enough to an installation to experience potential effects from, for example, noise, electromagnetic emissions or physical interaction with devices. The report does not make any attempt to consider the nature or consequences of these effects. Consequently, the report focuses on migratory behaviour in coastal waters during the outward and return migrations. This information is required for robust and defensible prediction of the risk of interactions between salmon and any proposed development. Regulators and other stakeholders also require accurate information in order to make strategic assessments of the risks to migratory fish in Scotland and beyond. At present, meeting these requirements is challenging because little relevant information exists. Gathering the relevant data empirically would be very difficult, because studies of salmon movements in open water are technically challenging and expensive. One alternative or complementary approach is to adapt hydrodynamic models for prediction of salmon migration under a range of specified conditions.

Hydrodynamic models are regularly used to assess the availability of tidal and wave energy resources and to predict potential changes to tidal flows. To understand migration, 'particle tracking models' (PTMs) can be used to simulate the trajectories of hypothetical particles

within hydrodynamic models; these 'particles' can be imparted with simulated biological behaviours in order to approximate the expected behaviour of salmon.

The main objective of this report is to assess whether PTMs represent a viable means of providing estimates of the potential for interactions between salmon and renewable energy developments. The report synthesises existing information on salmon migration in the Scottish context and explores PTM methods for simulating salmon migration. Additionally, the results of a disparate historical set of experiments on the movements of tagged salmon in Scotland have been formalised, compiled and scrutinised to establish whether the resulting data set constitutes an informative resource for understanding salmon movements in Scottish waters.

We conclude that hydrodynamic models have several advantages for estimating likelihood of passage through array locations, particularly in the case of the Pentland Firth:

1. A range of underlying hydrodynamic models may already be available.
2. In the absence of empirical data, modelling would allow exploration of the effects of different behaviours and tidal or meteorological conditions on encounter rate.
3. Modelling may allow hydrodynamic changes resulting from turbine operation to be predicted.
4. The approach has potential to generate hypotheses for testing in the field.

In order to facilitate the development of suitable particle tracking models, we suggest three activities:

A. Implementation of a high resolution particle-tracking model for the Pentland Firth.
B. Implementation of a larger-scale particle-tracking model covering near-coastal areas of the North Sea and the North Atlantic, in order to simulate outward migration of post-smolts and return migration of adult salmon through Scottish coastal waters.
C. Collection of empirical data to support the above modelling activities.

For A, an illustration of one potential application of this approach is provided for migrating salmon (it should be noted that this is not intended to represent an actual impact assessment). For this initial demonstration, most attention was given to eastward movement through the Pentland Firth, representing the return migration of adult salmon along the north coast of Scotland and into the North Sea. The outputs demonstrate that it is

possible to use hydrodynamic models to produce i) information on the probability of migrating salmonids passing through specific development sites; ii) estimates of the relative number of potential encounters with arrays positioned in a variety of locations; and iii) estimates of cumulative encounter rates where there are multiple arrays. Several improvements are suggested that would be required to develop this approach into a useful tool for impact assessment. The report also makes recommendations for methods and topics to be addressed under activities B and C.

A broad literature review identifies the most likely mechanisms underlying the migration of Atlantic salmon in Scottish coastal waters. Based on this review, a parsimonious conceptual model of coastal migration is provided, although since there is little direct evidence, it must be regarded as provisional, to be refined or replaced according to any new evidence.

The conceptual model requires that:

1. Migrating smolts have an innate directional preference that is approximately reversed in returning adults.
2. Salmon have an approximate sense of latitude based on a geomagnetic sense.
3. Smolts imprint to the latitudinal position of their home river and also to their point of departure from the coast.
4. Salmon have a sense of the coastal profile and align to it in the coastal domain.
5. Smolts imprint to home river odours.

A series of historical reports on the results of tagging of adult salmon, containing a large number of observations, have been digitised and geo-referenced. Overall, the geographical coverage of the data is extensive. These data are potentially a valuable resource for assessing migratory movements. In addition, data on recaptures of adults from tagging of smolts carried out in a number of key rivers on the east coast of Scotland (Rivers Tay, N. Esk and Dee) have been compiled in the same way. Together, these datasets constitute approximately 3400 records for the recapture of tagged fish.

These data are now available to develop a fuller understanding of migratory routes. This can be approached in two ways.

1. Visual assessment of patterns of distribution and movement of tagged adult salmon.

2. Numbers of fish caught in different fishery districts could be incorporated in a probabilistic, cellular model for spatial distribution which has also been devised.

The latter approach will support i) improved knowledge of salmon migration, ii) hypothesis formulation and iii) more robust understanding of potential interactions between salmon and marine developments.

These outputs are likely to be of immediate value to a diverse set of stakeholders, including technology developers, conservation agencies and regulators. Furthermore, any new biological insights from empirical studies will strengthen the modelling approach and extend the range of contexts to which it can be applied with confidence.

Chapter 1. Introduction

1.1 Marine renewable energy in Scottish seas

In response to rising global CO_2 emissions and the consequences for climate change and ocean acidification, governments worldwide have committed to various targets for emission reductions, energy efficiency increases, and generation of electricity from clean, renewable energy technologies. The European Union has committed to a legally binding target of producing 20% of EU-wide energy consumption from renewable sources by 2020[1], with the UK committed to generating 15% from renewables by this time (DECC 2012). Scotland has gone further, setting the ambitious goal of producing the equivalent of 100% of Scotland's electricity demand (and 11% of its heat energy demand) from renewables on the same timescale (Scottish Government 2012). Progress towards meeting these targets will involve so-called 'marine renewables' – offshore wind, wave and tidal power. Scotland is well positioned to lead the way in developing these energy sources, having substantial wind, wave and tidal energy resources (ABPmer 2008). Offshore wind is currently the most developed technology, with some offshore wind farms already operational within Europe; wave and tidal energy sources have yet to be harnessed on a commercial scale anywhere in the world. Since these technologies are still under development, the potential environmental implications of their deployment are poorly understood.

Some countries, including Scotland, have already identified promising locations for marine renewable energy. In particular, the Pentland Firth and Orkney Waters area is a key location for the future development of wave and tidal power, and several sites have already been leased by the Crown Estate (Appendix). However, in order to be sustainable, these and future developments must be partnered with robust assessment of any risks to the natural environment. This includes potential effects on fish species.

1.2 Atlantic salmon

The Atlantic salmon (*Salmo salar*) is an iconic species of high conservation significance and considerable socio-economic importance around the coasts of Scotland and within many Scottish river catchments. Improving our understanding of the biology and migratory

[1] Directive 2009/28/EC of the European Parliament and of the Council, 23rd April 2009 http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:32009L0028:EN:NOT (accessed 06/03/2013)

behaviour of these iconic and economically valuable fish is particularly important because of apparent long-term declines in the abundance of the species throughout much of its range, and the possibility of overlap between coastal migratory routes[2] and marine renewable energy development sites.

Salmon are anadromous, meaning that they spend the majority of their adult lives in the oceans but return to freshwater to reproduce. After hatching, young fish spend from one to four years living within the river as 'parr' before undergoing the physiological changes required to survive in saline waters (a process known as 'smoltification') and migrating to the ocean (at which stage they are referred to as 'smolts'). Smolts and post-smolts undertake a long-distance migration to feeding grounds in the North Atlantic which, for Scottish fish, include areas as far distant as the western coasts of Greenland (Jensen & Lear 1980). The feeding phase typically lasts for up to three years, after which the adult fish return to their rivers of origin to spawn. Fish that return after one winter at sea are known as 1 sea-winter (1SW) fish, or 'grilse', while those spending multiple winters at sea are referred to as multi-sea-winter (MSW) fish. After spawning, surviving fish (known as kelts) may return to sea for a further period before potentially spawning again, although repeat-spawners are infrequent in Scottish rivers.

Atlantic salmon stocks are considered to have declined throughout their range, particularly since the mid- to late- 1980s (Chaput 2012). However, most studies of abundance have been

[2] The term "routes" is commonly used in the published scientific literature on the migration of salmonids and other species to describe average spatial patterns of movement against the terrestrial frame of reference. In general, the use of the term "route" should not be taken to imply habitual or customary use of particular parts of the available marine space by salmon because it is not likely that they migrate along prescribed trajectories. Instead, the tracks achieved by individuals will result from orientated swimming activity expressed in a medium that itself moves in response to ocean currents, tides and winds. In some locations where movement or behaviour is spatially constrained, (for example by a common starting point, by convergence on a common destination, by terrestrial features such as islands or promontories or by behavioural barriers such as those related to temperature), the tracks of individuals will tend to coalesce. The resulting patterns of common spatial use will then constitute routes, (for example, as observed and exploited by fishermen), but only as an emergent feature of the behaviour of individuals. The concept of routes will be less useful in unconstrained locations where individual fish may achieve widely separated tracks and emergent patterns of common spatial usage may be absent or, at least, not discernible.

carried out at regional or stock-complex levels and some populations will be under-performing compared to the average trends (Chaput 2012). Almost 90% of the healthy river stocks of wild salmon are found in only four countries – Norway, Iceland, Scotland and Ireland (WWF 2001). Even within this core group, some stocks and stock components are in marked decline (Youngson et al. 2002; Vøllestad et al. 2009). Salmon are present in rivers across Scotland, which support stocks of national and international importance. Eleven rivers are designated Special Areas of Conservation (SAC) specifically for salmon, and salmon are a qualifying feature at an additional six sites (Malcolm et al. 2010).

Wild Atlantic salmon are also economically important; estimates in 2002 suggested that salmon and sea trout angling in Scotland contributed around £80 million of economic output, leading to around £39 million of income to Scottish households and supporting an estimated 2200 jobs (Radford et al. 2004).

1.3 Environmental Impact Assessment for salmon and proposed developments

Developers need to make robust and defensible predictions of the risk of impact on salmon from any proposed development. Regulators and other stakeholders also require accurate information in order to make strategic assessments of the risks to migratory fish in Scotland and beyond. These needs are typically met via the Environmental Impact Assessment (EIA) process. There are several factors that need to be considered in order to assess the risk to migratory fish, which could be approached via a three-stage, hierarchical process:

Stage 1 – Estimation of the numbers of fish that pass through a region of interest for development.

Stage 2 – Estimation of the numbers of those fish passing through a region of interest which also enter specific locations of proposed developments.

Stage 3 – Estimation of the actual rates of interaction with devices for fish passing through array locations, and the biological consequences of these interactions for individual fish.

However, limits to existing knowledge mean that there is great uncertainty regarding the numbers of fish passing through specific regions or proposed development locations (Stages 1 and 2). There are a number of questions that need to be answered in order to improve the

assessment of the numbers of fish passing through the Pentland Firth and other areas of interest:

- What routes do out-migrating smolts take when they leave their natal rivers?
- At what points in coastal waters do returning adult fish arrive?
- What routes do adult fish take from these points to their natal rivers?
- How do fish behave during the coastal phase of their migration?
- To what extent do migratory routes, timings or behaviours vary with river of origin?
- How will trajectories through specific areas be affected by water movements, particularly in extremely tidal channels such as the Pentland Firth?

At present, limited empirical information exists to answer any of these questions. This lack of information makes it difficult for developers to produce a thorough assessment of the possible impact of any development on salmon, regardless of what can be inferred, or assumed, about collision risk itself. Unfortunately, resolving these questions empirically will be very difficult, because studies of salmon movements in open water are technically challenging and expensive. Observations may also be location-specific, meaning that repeated experiments in multiple locations would be required. As a result, it may take many years to generate the required information using a direct, empirical approach.

An alternative or complementary approach is to adapt hydrodynamic models for prediction of salmon migration in specified conditions and for specific locations. Hydrodynamic models are widely used to simulate water movements at a range of scales, and may be readily available for marine renewable energy development sites, where they are already used to assess tidal and wave energy resources and to predict potential changes to tidal flows resulting from device deployment. In particular, 'particle tracking models' (PTMs) can simulate the trajectories of hypothetical particles within hydrodynamic models; these 'particles' can be imparted with simulated biological behaviours in order to approximate the expected behaviour of salmon. Model output can also be used to inform, focus and prioritise new field research and data collection. In turn, the incorporation of new insights from real-world data into models will make them more robust.

The main objective of this report is to assess whether PTMs represent a viable means of providing estimates of the potential for interactions between salmon and renewable energy developments. The report synthesises existing information on salmon migration in the

Scottish context and explores PTM methodologies for estimating the passage of salmon through marine renewable energy development areas. Additionally, the results of a disparate historical set of experiments on the movements of tagged salmon in Scotland have been formalised, compiled and then scrutinised to establish whether the resulting data set constitutes an informative resource for understanding salmon movements in Scottish waters. This is particularly important since these data (along with the data published by Potter and Swain, 1982) represent the only direct observational data available in this context. Currently, therefore, they offer the only direct biological driver for model development that is available and the only independent means of assessing model output.

1.4 Structure of report

Chapter 2 introduces particle tracking models, describes how these have already been applied to animal movements and explores how they might be adapted to address relevant questions. **Chapter 3** is an illustrative account of the initial implementation of a particle modelling approach to salmon migration through the Pentland Firth. **Chapter 4** contains a synthesis of the current state of knowledge of migratory mechanisms of salmon; these mechanisms could ultimately be included in particle tracking models in order to impart biological realism to simulations. The availability of large quantities of salmon tagging and recapture data collected in Scotland over the last 150 years potentially represents an important additional resource for examining migratory routes of salmon in Scottish coastal waters (Malcolm et al. 2010). **Chapter 5** includes a summary of the now extended data set and presents an outline for how these data could be consolidated and analysed. Finally, **Chapter 6** is a summary of the conclusions of the report, along with recommendations for future progress.

Chapter 2. Particle-tracking models: A potential tool for assessing salmon migration

2.1 Eulerian hydrodynamic modelling

Eulerian hydrodynamic modelling is a well-established methodology for simulating water movements, with a long history of use in oceanographic science. The scale of such models can vary immensely, ranging from circulation over the entire world ocean (eg. Masumoto 2010) to the flow of water in an individual river (eg. Liu et al. 2011). The outputs of this type of model are time-varying fields of vector data, which describe the movement of water across the whole model domain.

2.1.1 Structured and unstructured grids

Flow is simulated at each 'time-step' (discrete intervals of time over which the model calculations are carried out) between elements on a grid (or 'mesh') which is overlaid across the region of interest. The flow equations are typically solved using either a 'finite difference' or a 'finite element' method. The differences between these calculation methods are not of particular importance here, but there are differences between the types of grid that are typically used for each method. Finite difference models often use uniform rectangular elements ('structured grids') to represent the model domain, while finite element models use 'unstructured grids' composed of a mesh of triangular elements which can vary greatly in size across the domain. Unstructured grids allow complex coastlines to be represented more accurately, while allowing for coarser resolution in other parts of the model domain where the flow is more regular. This avoids the computational expense of using the highest resolution (needed for the most complex areas of coastline) across the entire model domain (Greenberg et al. 2007). Variable resolution can also be accommodated in structured grids by deforming or stretching the grid so that cells are smallest at the coast or near other features of interest (see Fringer et al. 2006), but this approach is much less flexible than using fully unstructured grids. There are some disadvantages to using unstructured grids; they can be more complex to code and require complex grid-generation procedures. Furthermore, while several grid generation methods are available (Greenberg et al. 2007), these may not automatically produce 'good' grids that represent the fluid environment accurately (Fringer et al. 2006).

2.1.2 Nesting

Increasing spatial resolution (modelling with smaller grid elements) is inappropriate without making similar increases in temporal resolution (by reducing time-step length), since processes occurring at smaller scales will also happen faster (Greenberg et al. 2007; Lacroix et al. 2009). This increases computational requirements for higher resolution models. This problem is particularly acute for unstructured-grid models; since it is not normally possible to vary time-step length across a model domain, the whole model must be run at the required time step of the highest resolution area of the model. This can be unnecessarily demanding on processing resources. One solution is to use nested models, where higher resolution model grids are used to simulate fluid movements in specific areas of a larger, coarser resolution model. Crucially, this allows the time-step to differ between different locations in the domain, since the higher resolution 'child' models can be run with shorter time steps than the larger scale 'parent' model. There are no theoretical limits to the number of levels of 'nesting' that can be simulated, and different types of model can be nested within each other. For example, a high resolution, unstructured-grid model can be nested within a lower resolution, structured-grid model to simulate fluid motions around complex coastal features within a larger, regional domain (Fringer et al. 2006).

The principal challenge with nested models is coupling the 'child' and 'parent' grids, which is complicated by the need to select one of several different coupling approaches (Fringer et al. 2006). Coupling can be one-way (output from the larger model is fed into the smaller, higher resolution nested grids, but processes within the smaller grids have no influence on the larger scale simulation) or two-way (where fluid motion in the higher resolution grids can feed back into the larger scale model). In addition, there are multiple ways of calculating how flows are translated across the boundaries between coarse and fine grids. Coupling of grids is further complicated where nested models are of different types (especially where unstructured grids are nested within structured grids).

2.1.3 2D and 3D modelling

Hydrodynamic models can be run as two-dimensional or fully three-dimensional flow simulations. Three-dimensional simulation is typically realised by dividing the water column into a series of layers in one of three ways (Greenberg et al. 2007): using fixed depths for the layer divisions (*z*-coordinate models - with thinner layers near the surface and/or the

seabed); using a fixed number of layers of variable thickness (σ-coordinate models); or by modelling the water column as a series of layers of constant density (isopycnal or ρ-coordinate models, though these are not useful in weakly stratified or well-mixed conditions).

Three-dimensional modelling is more computationally demanding, with little benefit for some applications; particularly in well-mixed waters, a 2D model may be sufficient. It is also possible to use a 'pseudo-3D' approach, which estimates the flow speed at any point in the water column by assuming that the 2D averaged velocity occurs at some pre-defined depth (typically around 70% of the distance from the seabed to the surface) and projecting a logarithmic velocity profile tending towards zero at the bottom (the boundary layer). This is sometimes known as using the 'law of the wall' (Willis 2011).

2.1.4 Forcing of models

An operational hydrodynamic model must account for a number of influences on water movement within the model domain. These are referred to as 'forcings'. A number of forcings can be applied, though which ones are important (and which ones can potentially be omitted) will depend on the system under consideration, the spatial scale of the model and the research questions that are of interest. Typical forcings include (see for example Bourque et al., 1999; Mork et al. 2012):

- **Meteorological forcing**. Wind has a key influence on water movements in most marine systems, and is commonly incorporated in hydrodynamic models. It is particularly important for large scale ocean general circulation models (OGCMs). Other meteorological conditions such as pressure and temperature can also be incorporated. Models can be forced either using 'climatological' data (a real time series of actual observations) or using 'synoptic' data (again, this uses real data, but in this case averaged over a period of time – for example, monthly wind speeds could be used averaged over a period of 10 years). Alternatively, data from atmospheric models can be used to force an oceanographic model.
- **Tidal forcing**. The importance of tidal influence in any hydrodynamic model will depend on the location being modelled. For example, tidal influences on large scale ocean circulation may be negligible compared to meteorological influences, and it is not uncommon for tidal forcing to be disregarded in OGCMs or other large scale simulations (Fossette et al. 2012). However, tidal influences are very significant in coastal waters, and in locations of interest to the marine renewable industry this

may be the dominant forcing. Tidal forcing can be incorporated based on real tidal data or on the output of larger-scale tidal models.

- **Topographical forcing**. In the open sea, over water depths of thousands of metres, the topography will have little impact on water movements, and again, this influence is often ignored in OGCMs. However, in models of coastal waters, the shape of the coast cannot be ignored. Under the principle of continuity, water constrained through a narrow channel, or pushed around a headland, will accelerate (Vogel 1994). Seabed topography (bathymetry) can exert a similar influence. Differences in 'bed roughness' (a characteristic of the seabed affected by material composition and bed form) will also affect water flows (Villaret et al. 2009). Accurate bathymetry is crucial for accurate modelling of hydrodynamic flows in shallow seas.
- **Wave climate** can also exert a significant influence in some systems (Jones & Davies 2001). Similarly to meteorological forcing, wave data can be used to force hydrodynamic models, and can be based on real time-series data or on the output of wave models.
- **Freshwater input**. Where large rivers enter the sea, this can have a locally important impact on hydrodynamics.

It is not sufficient to consider only the domain encompassed by the model itself, particularly where this is limited to a smaller area (Jones & Davies 2001); there will be influences from larger scale processes. Therefore, the 'boundary conditions' of a model must be set. How the model boundaries respond to fluid movements from within the model domain is also important. Boundaries can be treated as open (non-reflective) so that computed fluid motions radiate out from the domain, or 'sponge layers' can be used to absorb outward-propagating signals – alternatively open boundaries can be forced using real observations or outputs from a larger scale model such as a basin-scale OGCM (Greenberg et al. 2007). Another strategy is to reduce the influence of boundary conditions by making the boundaries as far away as possible from the actual area of interest (Lacroix et al. 2009) – in other words by making the model domain as large as possible. However, larger domains inevitably increase the computational requirements. In any case, applying appropriate boundary conditions to oceanographic models is critical in producing useful results (Fringer et al. 2006).

2.1.5 Hydrostatic versus Non-hydrostatic modelling.

Hydrodynamic models simulate pressure fields consisting of two components – hydrostatic (pressure resulting from the weight of the water column) and non-hydrostatic (additional

pressure resulting from fluid motion). For large scale models (such as OGCMs) the non-hydrostatic component can be relatively safely ignored, but it becomes very important as grid resolution increases. Consequently, high resolution models which do not account for non-hydrostatic influences may lead to erroneous or misleading results (Fringer et al. 2006). Some models (such as SUNTANS and DELFT3D; Tables 2.1 and 2.2) explicitly account for non-hydrostatic effects, however, the computational requirements are much greater than for more simple hydrostatic models – especially when it is considered that non-hydrostatic effects may only be important in particular areas of a model domain.

2.1.6 Water quality modelling

Hydrodynamic models can also incorporate simulation of additional properties of the marine environment in addition to fluid movements. Some aspects of water quality such as temperature (Bourque et al. 1999) or dissolved compounds (Scholz et al. 1976) have been proposed as possible cues for migrating salmonids, and these could be important to incorporate in models (particularly where riverine inputs may provide directional cues for Atlantic salmon; Section 4.10).

2.1.7 Validation of hydrodynamic models

In order to have confidence in the accuracy of hydrodynamic model outputs, it is necessary to validate them against real data. These data can come from a variety of sources, such as:

- **Tide gauges**. Predictions of tidal elevations from a model can be compared to time-series of data from tide gauges. The UK Strategic Tide Gauge Network includes 45 Class A tide gauges, data from which are freely available from the British Oceanographic Data Centre (BODC). However, only one gauge (Wick, 58.26N, 03.08W) is located in the vicinity of the Pentland Firth (for example). The Environmental Research Institute currently operates additional tide gauges (one at Scrabster, one at John O'Groats and one on the island of Stroma) which could be used in validation of future models.
- **Satellite measurements**. As an alternative to the use of tide gauge data for comparison with model outputs, satellite observations of tidal elevation (where available at suitable resolution) can be compared with modelled elevations, or used to generate estimates of surface currents that can be compared with modelled outputs (Fossette et al. 2012).
- **Direct current measurements**. Measurements of currents can be compared to flow fields output by a model. Current measurements are obtained using:

  - Acoustic Doppler Current Profilers (ADCPs). Moored, upward-looking ADCPs can show temporal trends at a particular point, and can be complemented by vessel-mounted downward-looking ADCPs which can sample current flows over a wider area. Some ADCP data is publically available; some is collected and held by developers and research institutes. Collation of this data could provide a valuable additional resource, and further ADCP surveys are likely to be beneficial.
  - High Frequency (HF) Radar. Shore based HF radar arrays use backscatter from the sea surface to measure surface currents and waves (Abascal et al. 2012). This can potentially cover a much wider area than would be feasible using ADCPs.
- **Observations of drifter tracks**. Floating drifters can be deployed, and their paths through a body of water can be compared to tracks predicted by Lagrangian particle simulations (Section 2.2; Hermann et al. 2002; Ohshima & Simizu 2008). Objects floating at the surface will be strongly affected by wind; this effect can be reduced by using drogues to ensure that buoys drift with currents rather than being driven by surface winds. In some circumstances, data are already available from large-scale drifter tracking experiments such as the ARGO programme (Fossette et al. 2012). Drifters have been a major tool in validation of large scale OGCMs, though few data are available at smaller spatial scales; site-specific experiments would need to be conducted.

Table 2.1 Hydrodynamic models known to have been used in particle tracking simulations and/or for modelling of highly tidal regimes such as the Pentland Firth. Examples of studies using each model, along with links to project websites (where available) are in Table 2.2.

							Prior published studies												
Model	**Type**	**Grid type**	**2D/3D**	**Integrated PTM?**	**Typical scale**	**Typical resolution**	**North Atlantic**	**British Isles**	**Scotland**	**Extreme hydrodynamics**	**Very High Resolution***	**Marine renewables**	**PFOW (or similar)**	**Particle-tracking**	**IBM**	**Vertical migration**	**Vertebrates (active swimming)**	**Salmonids**	**UK salmonids**
Ocean Circulation and Climate Advanced Model (OCCAM)	Academic	Structured	3D	No	Ocean basin	1/12°	■	■						■	■	■	■	■	■
Regional Ocean Modelling System (ROMS)	Academic	Structured	3D	No	Ocean basin	1/12°	■	■						■	■	■	■	■	■
Model for Applications at Regional Scale (MARS)	Academic	Structured	3D	No	Regional	4km	■							■	■	■			
Princeton Ocean Model (POM)	Academic	Structured	Both	No	Very variable	200m to >>5km	■	■	■	■		■	■	■	■	■	■	■	■
Semi-spectral Primitive Equation Model (SPEM)	Academic	Structured	Both	No	Regional	4km								■	■	■			
Spectral Element Ocean Model (SEOM)	Academic	Unstructured	3D	No	Global	25km	■							■					
Nucleus for European Modelling of the Ocean (NEMO)	Academic	Structured	3D	No	Ocean basin	1/4°	■							■	■	■	■		
Ocean Parallelise (OPA)	Academic	Structured	3D	No	Regional to Global	1/8°	■							■	■	■	■		
Ocean Surface Current Simulator (OSCURS) †	Academic	Structured	2D	No	Ocean basin (Pacific)	90km	■	■	■					■	■	■	■	■	■
HYbrid Coordinate Ocean Model (HYCOM)	Academic	Structured	3D	No	Regional to Global	1/12°	■							■	■	■	■		
Semi-implicit Eulerian-Lagrangian Finite Element (SELFE)	Academic	Unstructured	3D	Yes	Local to Regional	n/a				■	■			■	■	■			
Second-generation Louvain-la-Neuve Iceocean Model (SLIM)	Academic	Unstructured	Both	No	Local to Global	n/a	■				■			■	■	■	■		
Ocean general circulation model For the Earth Simulator (OFES)	Academic	Structured	3D	No	Regional to Global	1/10° to 1/30°	■							■	■	■	■		
Modular Ocean Model (MOM)	Academic	Structured	3D	No	Regional to Global	1/10°	■							■	■	■			
Miami Isopycnic Coordinate Ocean Model (MICOM)	Academic	Structured	3D	No	Ocean basin	1/12°	■	■	■					■	■	■			
Hamburg Shelf-Ocean Model (HAMSOM)	Academic	Structured	3D	No	Regional	18km	■	■	■					■	■	■			
Rossby Centre Ocean circulation model (RCO)	Academic	Structured	3D	No	Regional	3.7km	■	■						■	■	■			
TELEMAC-MASCARET	Commercial	Unstructured	Both	Yes	Local to Regional	n/a	■	■	■	■	■	■	■	■	■	■	■	■	■
MIKE	Commercial	Unstructured	Both	Yes	Local to Regional	n/a	■	■	■	■	■	■	■	■					
Stanford Unstructured Nonhydrostatic Terrain-following Adaptive Navier-Stokes Simulator (SUNTANS)	Academic	Unstructured	Both	No	Local to Regional	n/a	■	■	■	■	■	■	■						
DELFT3D	Commercial	Structured	Both	Yes	Local to Regional	n/a	■	■	■	■	■	■	■	■					
River and Coastal Ocean Model (RICOM)	Academic	Unstructured	3D	No	Local to Regional	n/a				■	■	■	■						
Unstructured grid Finite Volume Coastal Ocean Model (FVCOM)	Academic	Unstructured	3D	Yes	Local to Global	n/a	■				■			■	■	■			

*Very High Resolution refers to models which have been applied to grids with resolutions in tens of metres, often using unstructured grids.

†The OSCURS model has been specifically designed for modelling of the Pacific basin and would not be suitable for applications outside of that geographic area

Table 2.2 Example studies using each of the models from Table 2.1, along with links to hosting websites (where applicable)

Model	Example study	URL
OCCAM	Booker et al. 2008	http://www.noc.soton.ac.uk/JRD/OCCAM/
ROMS	Mork et al. 2012	http://www.myroms.org/
MARS	Ayata et al. 2010	
POM	Bourque et al. 1999	http://www.aos.princeton.edu/WWWPUBLIC/htdocs.pom/index.html
SPEM	Hinckley et al. 1996	
SEOM	Batchelder 2006	https://www.rsmas.miami.edu/users/miskandarani/SEOM/seom_index.html
NEMO	Scott et al. 2012	http://www.nemo-ocean.eu/
OPA	Hays et al. 2010	
OSCURS	Bracis and Anderson 2012	http://www.pfeg.noaa.gov/products/las/OSCURS.html
HYCOM	Putman et al 2012	http://hycom.org/
SELFE	Liu et al. 2011	http://www.stccmop.org/CORIE/modeling/selfe/
SLIM	Hamann et al. 2011	http://sites.uclouvain.be/slim/
OFES	Zenimoto et al. 2011	http://apdrc.soest.hawaii.edu/datadoc/ofes/ofes.php
MOM	Kim et al. 2007	http://mom-ocean.org/web
MICOM	Paris et al. 2005	http://gcmd.nasa.gov/records/RSMAS_MICOM.html
HAMSOM	Heath & Gallego 1998	http://www.ifm.zmaw.de/research/models/hamsom/
RCO	Corell et al. 2012	
TELEMAC-MASCARET	Herbert et al. 2012	http://www.opentelemac.org/
MIKE	Easton et al. 2012	http://www.dhisoftware.com/
SUNTANS	Baston and Harris 2011	http://www.stanford.edu/group/suntans/cgi-bin/index.php
DELFT3D	Symonds 2011	http://www.deltaressystems.com/hydro/product/621497/delft3d-suite
RICOM	Plew & Stevens 2013	
FVCOM	Tian et al. 2009	http://fvcom.smast.umassd.edu/FVCOM/index.html

2.2 Lagrangian 'Particle tracking' models within a Eulerian framework

Lagrangian models (also known as 'particle tracking' models, or PTMs) provide a method of tracking hypothetical 'particles' within the vector fields generated by Eulerian hydrodynamic models. While dispersion of some substances is conventionally simulated directly within Eulerian models, others, such as pollutants (Elliott et al. 2001; Periáñez & Pascual-Granged 2008; Soomere et al. 2011) including oil (Ohshima & Simizu 2008; Díaz et al. 2008) or floating plastic debris (Isobe et al. 2009; Yoon et al. 2010; Kako et al. 2011; Lebreton et al. 2012) are often simulated using PTMs. Given the increasing availability and decreasing cost of computing power, the trajectories of relatively large numbers of particles can be simulated, overcoming statistical concerns relating to low sample sizes (Willis 2011; Simons et al. 2013). Often these models are much simpler and quicker to run than the underlying hydrodynamic models, and are typically run 'offline'; the hydrodynamic model is run first, and then the PTM is run using the stored output from the hydrodynamic model to compute the trajectory of particles placed within the model domain. Fully dynamically coupled Eulerian-Lagrangian models are possible (e.g. Soomere et al. 2011) but are less commonly

applied, potentially because of the greater computational requirements, and for many applications there would seem to be little advantage to this method.

Commercial hydrodynamic models (such as MIKE and DELFT3D, see Table 2.1 and 2.2) sometimes have integrated particle-tracking modules which can be used directly to run particle-tracking simulations on their outputs. These may be initially simpler to use, but since the models are not open source, the particle tracking routines may not be sufficiently flexible for simulating actively swimming organisms (Section 2.3) with a range of possible behaviours. There are also freely available tools (for example ICHTHYOP[3] and TRACMASS[4]) which can be used to run PTMs on the outputs from separate Eulerian models, although in some cases they can only work with outputs from specific hydrodynamic models. For example, ICHTHYOP is designed to run on outputs from ROMS, MARS, or NEMO (Tables 2.1, 2.2) models – however it may be possible for experienced users to modify the code to accommodate data from other models. An alternative approach is to create proprietary particle tracking code for particular applications, which may allow for greater flexibility, but obviously requires a higher level of expertise and initial effort.

2.2.1 Advection

Once particles are released into the model domain, they are moved in accordance with the flow velocity at their location at each time step. This is termed advection. The length of time step used will vary depending on factors such as the spatial resolution and intended application of the model. Studies of particle movements in large-scale circulation models (such as OGCMs) can have hourly (e.g. Corell et al. 2012) or even daily (e.g. Pous et al. 2010) time steps but this is inadequate for simulating the motion of particles in high flow conditions, where time steps on the order of minutes (e.g. Domingues et al. 2012) or even seconds (e.g. Herbert et al. 2012) may be more appropriate.

The simplest scheme for advection directly imparts the velocity and direction of the flow at the particle's position to the particle itself. This is known as the 'Forward Eulerian' advection scheme, and while computationally the simplest option, it is known to be less reliable than other schemes (Qiu et al. 2011; Willis 2011). A number of other advection schemes are possible (Gräwe 2011) and in particular the fourth-order Runge-Kutta (RK4) integration

[3] http://www.brest.ird.fr/ressources/ichthyop/index.php
[4] http://tracmass.org/

method is well regarded and commonly used (Willis 2011). This involves interpolating the velocity half way between a particle and the 'destination' (the point it would have been advected to under a Forward Eulerian scheme) four times per time step. This produces more realistic outcomes, especially around complex coastlines; although it is more computationally intense this trade-off is considered justified and use of RK4 integration is recommended (North et al. 2009). Some Lagrangian modelling tools have a built-in capability to use RK4 (e.g. ICHTHYOP; Lett et al. 2008). Another promising advection scheme is the Adams-Bashforth-Moulton predictor-corrector scheme (Simons et al. 2013) which is claimed to perform similarly to the RK4 scheme, but with somewhat reduced computational costs (Qiu et al. 2011).

Many particle-tracking models are also modified to include a small random displacement. This approximates turbulent processes occurring below the grid scale of the model, and is often incorporated as a simple random walk process based on the diffusivity of the medium being simulated. This results in an improvement of the reliability of PTMs (Willis 2011), and some authors even contend that including this in models removes the need for RK4 integration (Adlandsvik et al. 2004). Other authors account for the effects of turbulence by explicitly including it within the particle advection scheme (Guizien et al. 2006), or by explicit modelling of turbulence within the hydrodynamic model itself, though this can be extremely computationally demanding. In three-dimensional (or 'pseudo-3D') models, vertical diffusion may also need to be included in a similar fashion (Guizien et al. 2006). Care must be taken when applying a random walk in a diffuse medium, since turbulent diffusion in the real world is non-uniform; this can lead to spurious modelling results if a random walk assumes uniform diffusivity. This can be compensated for by adjustment to the way in which a random walk is calculated (Visser 1997).

2.2.2 Analysing the outputs

There are several approaches to analysing and interpreting PTM outputs, and the best approach will depend on the research goals. The most basic approach is simple qualitative description of particle trajectories in relation to particular features of interest, but this is impractical where large numbers of particle trajectories have been simulated. For a more robust approach, densities of particle positions (either final locations, or locations at any time point in the model) can be explored using kernel density estimators (KDEs), a type of

probability density function which describes the probability that particles will pass through a given location or area, generating useful contour maps of particle passage density. A somewhat simpler alternative is the use of so-called 'Lagrangian targets' (Willis 2011). These are hypothetical points, lines or areas within the model; when the simulation is run the number of particles encountering these features is recorded. This can be used to determine the proportion of particles reaching a coast (Soomere et al. 2011), crossing a line of latitude or longitude (Kettle & Haines 2006; Kim et al. 2007), escaping from an estuary (Herbert et al. 2012), or (of more direct relevance here) passing through defined areas (Bourque et al. 1999; Pous et al. 2010; Herbert et al. 2012).

2.2.3 Backtracking

PTMs can also be run in reverse, which is known as inverse modelling, or backwards-in-time tracking (BITT). The same hydrodynamic model outputs are used, but this time the movements are calculated using a reverse advection process. This approach can be used to estimate the likely point of origin of objects arriving at a site (Isobe et al. 2009). It becomes more complicated if any form of random walk process is used to simulate sub-grid scale turbulence (Thygesen 2011), as a random walk cannot be reversed in time, and particles which in reality dispersed from a single point will not converge on this point in a reverse simulation. There are statistical approaches to deal with this problem, such as running a series of BITT and FITT (forward-in-time tracking) models in combination (Batchelder 2006), but in general, backtracking is less likely to be a primary methodology in the case of salmon migration modelling.

2.2.4 Variability

When simulating real-world systems, it is important to be aware that these are not static, unchanging systems. Variation in hydrodynamic, oceanographic or meteorological factors over various timescales can lead to substantial seasonal or inter-annual variation in the trajectories of passive particles (or other advected tracers) in both observed and simulated systems (Karcher et al. 2004; Ohshima & Simizu 2008; Orre et al. 2008; Mariani et al. 2010; Hays et al. 2010). Therefore it may prove necessary to run a number of repeat simulations to explore potential effects of variation in environmental conditions on particle trajectories.

2.2.5 Validation

The reliability of particle-tracking simulations is tested by validation of the underlying hydrodynamic model (Section 2.1.7), or by comparing simulated drifter tracks with the trajectories of drifters deployed in the real-world system. The advantage of this latter approach is that it provides some validation to the underlying Eulerian model as well as the Lagrangian PTM itself.

2.3 Individual-Based or Agent-Based modelling (IBM/ABM)

One of the advantages of Lagrangian particle-tracking methods for marine ecology is that in addition to the influence of external forcings, behavioural rules can be applied to individual particles in order to approximate the movements of animals or their eggs/larvae. Most organisms do not behave as entirely passive particles (e.g. Kimura et al. 1999; Azumaya & Ishida 2004) even in high flow systems (Kemp et al. 2008), and seemingly minor deviations from total passivity can have a strong influence on trajectories in PTMs (Putman et al. 2012; Scott et al. 2012). The application of behavioural rules to particles is known as individual-based modelling (IBM) or agent-based modelling (ABM), although some authors reserve the latter term for models which explicitly account for behavioural interactions between individual particles, which will not be considered further in this review. The strength of IBMs is that they can be used to test hypotheses about movements of animals in the sea, such as mechanisms used for navigation and orientation. The majority of particle tracking IBM studies have focused on dispersal of eggs and larvae; however, an increasing number of papers concern larger animals including turtles (e.g. Putman et al. 2012) and fish (e.g. Mork et al. 2012; Bracis & Anderson 2012).

Many organisms show marked vertical migration behaviour, often in response to tides or to the day/night cycle. Even in the absence of active horizontal displacement, differences in transport depth (or changes in depth with time) can lead to significant changes in horizontal trajectories in both hydrodynamic models and real-world systems (Hinckley et al. 1996; Adlandsvik et al. 2004); it is therefore crucial to account for vertical behaviour in this kind of model. Hinckley et al. (1996) were able to obtain reasonable, though imperfect, correspondence with distributions of sampled fish larvae (in this case walleye pollock, *Theragra chalcogramma*) using a hydrodynamic model incorporating only vertical swimming behaviour. However, in addition to moving vertically, larger animals are also capable of

active horizontal movement. Their actual trajectories will therefore be a combination of displacement resulting from hydrodynamics and their own powered motion.

IBMs allow the incorporation not only of consistent behaviour, but also of behaviours that vary spatially or temporally. The simplest variation in behaviour is vertical migration (see above), but individuals may also have different activity levels and swimming speeds at different times. Such variation in swimming speed and direction can affect the overall spread of particles in a modelled system (Hamann et al. 2011). Alternatively, individuals may respond to variation in current speed or direction. Such variation includes changing orientation in different flow conditions, avoiding areas of greater flow acceleration (Kemp et al. 2008), or engaging in selective tidal stream transport (STST) by taking shelter at the sea bed (for example) when the current is going the 'wrong' way (Harden Jones et al. 1979).

2.3.1 Incorporating specific behaviours into IBMs

Incorporating individual behaviours (and variation in behaviour) into models is distinct from understanding the root cause of those behaviours (but see Box 1). In general, simpler rules are preferable from a modelling standpoint, and can often produce realistic patterns (Walter et al. 1997). The most common method used to simulate the active movement of animals is the correlated random walk (CRW) (Codling et al. 2008; Willis 2011). The course taken by an individual undertaking a CRW is calculated on the basis of four properties which are applied to each individual (particle) in the model:

1. The present position of the animal
2. The present heading of the animal
3. An error term describing the tendency of the animal to maintain its present heading (sometimes referred to as 'directedness' or 'steadfastness')
4. A velocity term (distance travelled per time-step)

At each time step the movement of the individual is calculated based on the above information. The degree of correlation in a CRW is determined by the error term. If the error term is zero, then the individual maintains a constant heading (and would therefore travel in a straight line in the absence of current-driven advection). If the error term is maximal then the individual is effectively adopting a fully uncorrelated random walk (UCRW). However, migrating animals do not wander across the sea in a random pattern, and it is necessary to

incorporate specific orientation or navigation mechanisms into a model in order to simulate their trajectories.

2.3.1.1 Land avoidance

One problem with introducing active swimming behaviours into hydrodynamic models is that individuals may make 'illegal' moves; for example, in coastal models individual particles may make moves that would put them on land. Therefore, land avoidance must often be explicitly incorporated into a model. There are several more or less simple means of achieving this:

- Particles encountering the coast can be reflected (potentially followed by a period of uncorrelated random walking before resuming prior behaviour) although exact reflection angles can be complicated to calculate on complex coastlines. This could be handled by giving particles a random heading away from land (Booker et al. 2008).
- Particles can return on their inbound trajectory. This would require a period of random movement afterwards to prevent the individual making the same move back onto land in the next time step.
- Particles encountering the coast can make a 90 degree turn, with a fixed or variable probability of left or right turn.
- Particles which would be advected onto land in any particular time step can 'miss a turn' and not be moved during that timestep (Adlandsvik et al. 2004).
- Coastal shear could be explicitly modelled to avoid trapping (Bourque et al. 1999).

2.3.1.2 Migration and Orientation

In some ways, modelling migrating animals is simpler than modelling non-migratory species, because it is possible (at least provisionally) to disregard foraging, territorial behaviour, and other non-migratory influences. However, the way in which this behaviour is incorporated in models (as distinct from how they navigate in the real world) is critical in ensuring that models are useful. It is preferable from a prediction or hypothesis-testing point of view if directed movement can be related to real-world cues. However, useful results may still be obtained without a detailed understanding of how exactly the animals make use of environmental information.

Box 1 A problem: modelling behaviours to fit data vs. using models to evaluate behaviours

Models of passive drift often do not generate good fits to observations, particularly for organisms which can exert some control over their trajectories. For large individuals with the capacity for long distance directed movements, significant vectors need to be built into models to account for this behaviour. It is easy, therefore, to succumb to the temptation to incorporate behaviours which simply allow the model to better represent the observed patterns without careful consideration of the biological plausibility of these behaviours.

Perhaps the most common example is the incorporation of a rheotactic response (either negative or positive) into models of fish migration. Negative rheotaxis (swimming on the same heading as the predominant direction of current flow) in particular has been used in several model studies and has in some cases resulted in a good fit to (for example) recaptures of tagged salmon post-smolts (Mork et al. 2012). Does this mean that real post-smolts demonstrate this behaviour? While it may be plausible for birds flying over land (which can use visual cues to assess wind-driven displacement and act accordingly), pelagic swimming fishes such as migrating salmon in the open sea will have no visual cues that they can use to assess current-induced displacement. Other cues would be required, and while there is evidence that salmonids possess a potentially sensitive geomagnetic sense, there is as yet no indication that this would allow them to make instantaneous assessments of their absolute displacement. Adult fish migrating through (relatively) shallow coastal waters might be able to use visual cues to measure displacement during the day in clear waters, but at depths greater than a few metres, during the night or in turbid waters other cues would be necessary. Rheotactic behaviours in this context thus seem biologically implausible, and their use in such modelling is of questionable value. In the absence of empirical evidence for rheotaxis under open water conditions caution is advised regarding this assumption, unless other cues can be identified that might be used as an external frame of reference to allow assessment of current-driven displacement. Furthermore, while a negative rheotactic (or even passive drifting) strategy would get Irish and Western Scottish fish to their destinations in the North Atlantic (Mork et al. 2012) it would not function for the east coast of Scotland, where the predominant coastal current flows are southwards.

Similarly, other studies adopt simple rules such as ‘swim on a fixed bearing’ or ‘navigate towards a certain point’ which can produce impressively compelling fish trajectory plots, despite lacking a thoughtful consideration of the means by which individual animals might adopt such strategies. Without this, the outputs may be of questionable validity.

Alternatively, we advocate an ultimately more useful approach, which is to use information derived from published literature and expert knowledge to propose a number of biologically plausible cues, orientation mechanisms, and migration strategies, which can then be applied in a modelling framework. These could then be tested against real world observations. In the case of situations such as the Pentland Firth, where no such observations exist, it is all the more important that any behaviours included in models are realistic.

Orientation is generally considered to mean a directional response to locally available environmental cues. One such cue in a hydrodynamic model is the current vector information from the hydrodynamic model itself. ‘Rheotactic’ behaviour is orientation based on currents (negative rheotaxis is swimming with the current, positive rheotaxis is

swimming against the current). Rheotaxis is relatively simple to incorporate in an IBM, by setting the heading of the particle based on the direction of advection by the hydrodynamic model. However, postulating rheotactic behaviour is problematic in the absence of cues on which an animal's assessment of current direction might be based (Box 1). However, in shallow waters, or for species that travel close to the seabed, rheotaxis may be an important determinant of rates and pathways of movement.

Other cues would have to be explicitly coded into models as either point sources (for example in the case of olfactory cues) or as spatially varying maps of cue levels (for example in the case of geomagnetic cues). This would necessitate coding rules into the simulation for how individuals would respond to different levels of the cue in question. In the real world animals may also use multiple cues to orient themselves in complex multi-cue landscapes, and this is potentially more complicated to incorporate in models.

Orientation can be incorporated into an IBM by modification of the CRW. One means of achieving this is via a biased CRW (Codling et al. 2008), incorporating a (potentially varying) tendency to move in a certain direction at each time step. This can introduce problems with navigating around obstacles, where a consistent bias can increase the likelihood of getting 'stuck' on coastal features. However, there are ways to reduce this problem, for example by implementing orientation behaviour only at certain time steps, or by programming a hierarchy of behaviours (Willis 2011) to be applied depending on circumstances (for example, if the particle comes into contact with the coast, land avoidance would be prioritised, while in other circumstances the particle may be free to undertake orientation behaviour). Changes in navigational strategy at particular times or places can also be implemented, by:

- changing direction/strength of orientation once a particular time step has been reached;
- changing direction/strength of orientation in response to reaching a threshold of some environmental cue;
- setting a series of navigational waymarks and programming navigational rules such that individuals orient towards to the next 'downstream' waymark in the sequence (Willis 2011); or
- defining particular 'navigation zones' within which individuals orient in a particular direction (Putman et al. 2012).

2.3.2 Validation

For particle tracking models of moving animals, in addition to validation of underlying Eulerian and Lagrangian models (Sections 2.1.7 and 2.2.5), it is also advisable to validate the assumptions and rules in an IBM by comparing projected trajectories with actual trajectories of tracked individuals (where suitable technology is available to record this information) or by comparing predicted locations of individuals at different times with empirical data such as results of plankton tows (for drifting plankton) or captures of tagged fish. Where possible, any behaviours attributed to animals in models should be verified by observations of animals in their natural environment. However, this is often difficult to achieve.

2.4 Applying PTMs to salmon migration

In the case of salmon migrating to and from their natal rivers and potentially passing through development sites, there are essentially two levels at which PTMs are most likely to be useful:

1. Large-scale modelling of the migratory pathways of outmigrating smolts and returning adults in order to evaluate the likelihood that they pass through areas where development is likely, and to predict the point of entry into the UK coastal system of returning adult fish (see Section 1.3).
2. Modelling the passage of salmon (both adults and smolts) through extreme tidal channels (for example the Pentland Firth) or other specific defined bodies of water, in order to estimate the probability of encountering arrays of renewable energy devices (particularly tidal energy devices) in these locations (see Section 1.3).

2.4.1 Modelling large-scale salmon migration in hydrodynamic models

It is known from previous tagging studies that salmon from Scotland do reach feeding grounds in the Western and Northern North Atlantic and that at least some of these fish pass close to the Faroe Islands as adults during the return migration (Hansen et al. 2002). Beyond that we do not have detailed information about the paths taken by these fish during the oceanic phase of their life-cycle, and their navigational mechanisms are uncertain (see Chapter 4). This provides an opportunity to use particle tracking approaches to explore these phases of the lifecycle. This has been done for other marine migratory vertebrate species in other locations (as well as in the North Atlantic) and these studies provide some instructive examples of how this might be approached for Atlantic salmon.

2.4.1.1 Passive drifting larvae – migratory eels

Eels are also migratory diadromous fish, but their lifecycle differs from salmon; adult eels migrate out to sea to spawn and the larvae make the return journey. Eels are economically important and have been widely studied in some locations, including via the use of particle tracking models in large-scale hydrodynamic models (Power & McCleave 1983). Most studies modelling trajectories of eels have focused on the return migration of the larvae (leptocephali) from the marine spawning locations to their home countries (Bonhommeau et al. 2009; Pous et al. 2010; Zenimoto et al. 2011), rather than on the outmigration of adults. They have been successful in simulating the real-world patterns shown by eel larvae while strongly reinforcing the significant influence of vertical position in the water column on the trajectories of drifting particles. While these studies do not involve any active horizontal swimming or navigation behaviour, they do demonstrate that particle tracking models can reproduce migratory pathways in large-scale models (including within the specific context of the North Atlantic). They also illustrate how PTMs can be used to test hypotheses about migratory behaviours, and to predict impacts of future changes, including periodic shifts in ocean circulation resulting from climate variation such as the El-Nino Southern Oscillation (Kim et al. 2007) or long term shifts resulting from climate change.

2.4.1.2 Turtles – movement of juveniles in ocean circulation patterns

Unlike eel larvae, turtle hatchlings are capable of sustained active horizontal swimming (up to 0.5 $m.s^{-1}$), and a number of modelling studies have attempted to explore their migratory pathways (Gaspar et al. 2012; Putman et al. 2012; Scott et al. 2012). It has also been hypothesised that they are able to navigate over long distances, and therefore these models illustrate the use of a number of movement and navigation strategies including:

- Passive drifting
- Random swimming direction at each time step (UCRW)
- Orientation to currents (negative rheotaxis)
- Orientation based on surface wind direction
- Navigation based on magnetic cues
- Mixed strategies

Movement strategies have been typically modelled using correlated random walks, but other approaches have been used, including variable navigation depending on which of several ‘navigation zones’ individuals are located in at each time step (Putman et al. 2012).

At least one investigation (Hamann et al. 2011) compared trajectories derived from more than one navigation or orientation approach. However, some of these studies exemplify the problem of assuming rheotactic behaviour (or other simple navigational rules) without strong justification that this is realistic (Box 1). While such studies can produce interesting results that compare well with observations of animal trajectories, they reveal little about how animals navigate and are less useful for hypothesis testing. They do still demonstrate that PTMs are useful for exploring long-range migration in actively moving animals, showing that random swimming has a significant impact on dispersion (Gaspar et al. 2012) and that even a modest degree of oriented swimming can exert a significant influence on migratory pathways (e.g. Putman et al. 2012).

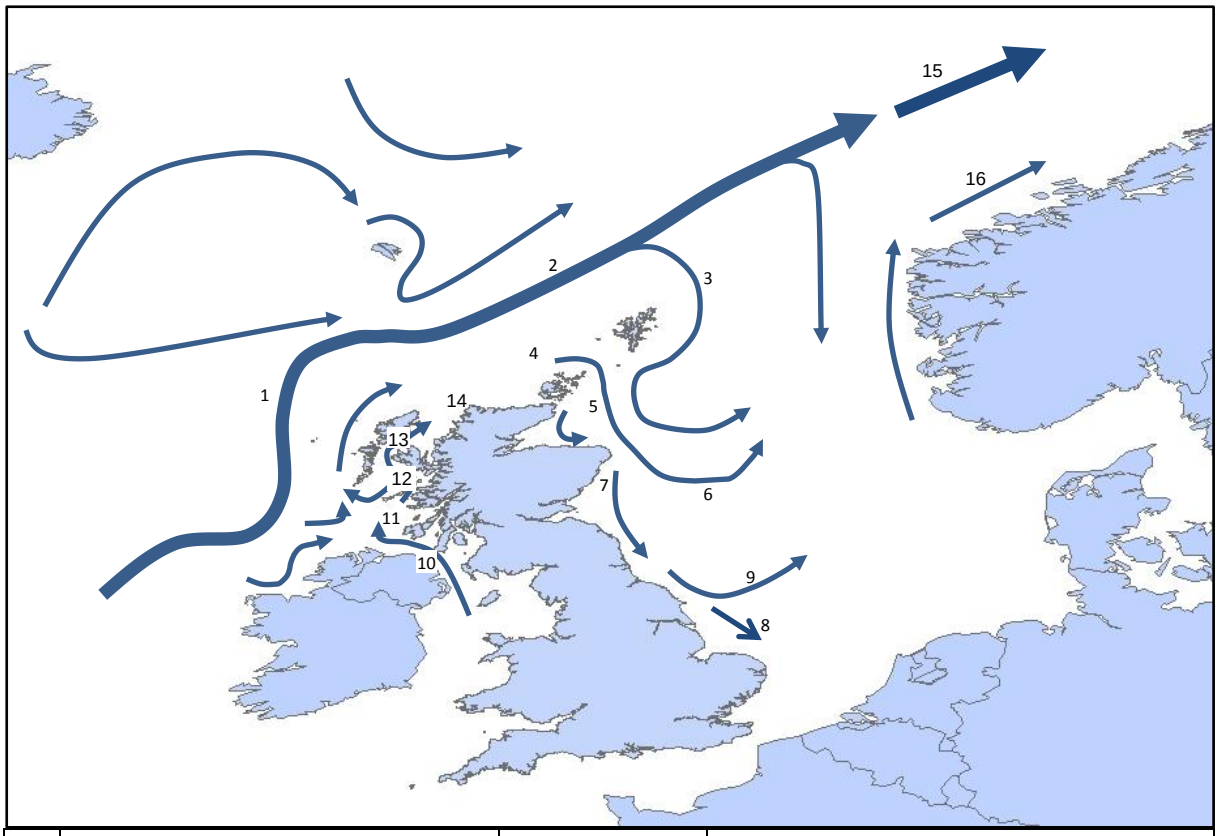
2.4.1.3 Pacific and Atlantic salmon – previous studies on adult and smolt migrations

To date, there have been a limited number of published studies that use particle tracking approaches to explore the long-range migration of salmonids, and most of these have concerned the return migration of adult Pacific salmon species (Bourque et al. 1999; Healey et al. 2000; Bracis & Anderson 2012), specifically chum salmon (*Oncorhynchus keta*), coho salmon (*Oncorhynchus nerka*) and chinook salmon (*Oncorhynchus tshawytscha*). Like Atlantic salmon, these species migrate out to distant marine feeding grounds before returning to their natal rivers to spawn, and may use similar navigational mechanisms. Models have also been used to study the migrations of pacific salmon post-smolts (Azumaya & Ishida 2004) and juveniles (Walter et al. 1997). Similar studies of Atlantic salmon migration are rarer, with only two published studies available, both on migration of smolts from Ireland and Norway (Booker et al. 2008; Mork et al. 2012). There have been no comparable modelling studies on the outmigration of post-smolts from Scottish rivers, and none on the return migration of adult Atlantic salmon.

Models of adult salmon migration not only represent individual animals with high maximum sustainable swimming speeds (≥1 $m.s^{-1}$), but also incorporate land-avoidance behaviours, since part of the migration occurs near to coasts. Because of their higher swimming speeds, hydrodynamic influences may be less significant for large fish, particularly in open water where current speeds may be comparatively weak. However, this may be life stage dependent. During directed migration the influence of currents may be negligible, while during the oceanic feeding stage (where movements may not be consistently directed if

there is no active navigation) surface currents may have a substantial effect on the location of individual fish. Indeed, ocean surface currents may be the primary influence on the locations of sockeye salmon (*O.* nerka) during the adult feeding stage of their lifecycles (Walter et al. 1997).

During early life stages (outward migration as post-smolts) the influence of large scale currents may be more substantial. On the continental shelf, migration paths of smolts may be driven by currents around coasts and within the North Sea (Fig. 2.1). The coastal circulation around the UK and within the North Sea has been studied extensively, largely as a result of the existence of a small number of sites at which radionuclides have been released into the ocean. The most important examples are the nuclear reprocessing facilities at Cap de la Hague (France) and Sellafield (Cumbria, England) and the facility at Dounreay on the North Coast of Scotland. Studies based on modelling of the dispersal of radionuclides from these sites (Kershaw et al. 1992; McCubbin et al. 2002; Gao et al. 2004), along with other oceanographic research (Turrell et al. 1990; Turrell 1992; Turrell et al. 1996), have revealed a predominantly clockwise 'residual' circulation (the average flow once tidal oscillation has been subtracted) around the north of the UK landmass (Figure 2.1); this is known as the Scottish Coastal Current (SCC). Passively advected tracers (simulated) originating from Dounreay appear to follow a trajectory around the North Sea/Eastern North Atlantic which may be similar to that taken by out-migrating smolts: to the north with the Norwegian Coastal Current (NCC/NwCC) and the Norwegian Atlantic Current (NwAC), with some subsequent passage southwards along the east Greenland coast.



	Current name	Residual velocity (cm.s^{-1})	Source of data
1	Slope current (up to Wyville-Thompson ridge)	12	UKMMAS 2010
2	Slope current	20	Winther & Johannessen 2006; UKMMAS 2010; Baxter et al. 2011
3	East of Shetland Atlantic Inflow	10	Turrell 1992; Turrell et al. 1996
4	Fair Isle Current (West of Orkney);	7	Turrell et al. 1990
5	Fair Isle Current (North Sea)	10	Turrell et al. 1990; UKMMAS 2010
6	Dooley current (or other Scotland to Norway Flow)	4	Furevik 2000; Gao et al. 2004; Kershaw et al. 2004; Winther & Johannessen 2006
7	Scottish Coastal Current (Pentland Firth to East Coast)	2	McCubbin et al. 2002; Gao et al. 2004; Kershaw et al. 2004
8	Scottish Coastal Current (Pentland Firth to East Anglia)	2	McCubbin et al. 2002; Kershaw et al. 2004
9	Central North Sea Water	2	Kershaw et al. 2004
10	North Channel (Irish Sea)	5	Davies et al. 2002; Kershaw et al. 2004
11	Scottish Coastal Current (Off Mull)	8	Hill & Simpson 1988
12	Scottish Coastal Current (South Minch)	6	Hill et al. 1997; UKMMAS 2010
13	Scottish Coastal Current (Minches)	4	Hill & Simpson 1988
14	Scottish Coastal Current (SCC) North Coast to Pentland Firth)	4	McCubbin et al. 2002; Kershaw et al. 2004
15	Norwegian Atlantic Current	35	Kershaw et al. 2004; Winther & Johannessen 2006
16	Norwegian Coastal Current	20	Haugan et al. 1991; Furevik 2000; Kershaw et al. 2004; Winther & Johannessen 2006

Figure 2.1 Schematic representation of the major oceanic or coastal currents in the North East Atlantic and the North Sea, modified from Baxter et al. 2011. Currents of relevance to this report are listed, with approximate mid-range estimates of residual current velocity derived from the literature.

However, passive drifting in the residual currents around the North Sea is not an adequate explanation of the paths taken by out-migrating smolts. Large proportions of smolts would be lost, since not all particles (even in models) are advected along the 'correct' path; some end up trapped in the Baltic Sea or dispersed into the Barents Sea (Kershaw et al. 2004), and models of drifting fish larvae find that only relatively low proportions drift towards Greenland after release north of Norway (Adlandsvik et al. 2004). More significantly, passive drift would be too slow to allow fish to complete the migratory cycle within a year; radioactive tracers take as much as ten years to reach the Greenland coast after release in UK coastal waters (Orre et al. 2008). This could be overcome, perhaps, by active swimming in the direction of currents (negative rheotaxis) and models including this behaviour for migrating smolts do appear to correspond with actual recapture positions of salmon smolts in the North Atlantic (Booker et al. 2008; Mork et al. 2012). However, the assumption that fish are able to follow currents in deep, open water is problematic (Section 2.3.1.2, Box 1). Additionally, seasonal and interannual variation in meteorological forcing can have significant influences on ocean circulation and thus on trajectories of advected particles (Orre et al. 2008; Olbert et al. 2010a; 2010b); this would make the trajectories of fish far less consistent from year to year if they were simply passive, or used rheotaxis to swim with currents. Modelling studies of Pacific salmon confirm that passive drifting is not sufficient to explain large-scale migratory patterns; modelling a directional swimming component which moved fish toward preferred temperatures better predicted sampled distributions of chum salmon, *Oncorhynchus keta* (Azumaya & Ishida 2004), although there are similar problems with assuming that fish are able to instantaneously assess the direction of large-scale temperature gradients.

Studies on Pacific salmonids have also explored the possibility that fish may use magnetic cues for migration. Simulated chinook salmon (*O. tshawytscha*) were able to navigate to the vicinity of their home river in the Pacific Northwest using geomagnetic information (Bracis & Anderson 2012). Model fish imprinted with the relevant geomagnetic cue (magnetic field inclination angle or intensity) as they left their natal river and then pursued a two-phase navigation strategy during the return home:

1. In the first phase they moved towards the isoline where the relevant magnetic cue matched that of their home river.

2. Once the isoline was reached, they tracked it eastwards until they struck the coast (at the home river).

Inclination angle was found to be the superior cue in this particular model (because it has smaller secular variation and is more robust to variability in return angles), but intensity was adequate (Bracis & Anderson 2012). One implication of an 'isoline-following' strategy would be that migrating fish may travel through relatively constrained 'migration corridors' where they would be particularly vulnerable to impact. Currently, however, there is no evidence that this actually occurs. It must also be noted that no additional evidence was presented that fish are actually able to obtain and use information about the geomagnetic field, and in particular to infer which direction they need to travel to get to the isoline during the first phase of navigation. However, a more recent study (Putman et al. 2013) has shown that the return migration of chinook salmon may indeed be guided by a geomagnetic mechanism (Section 4.9). This provides a rather neat picture for one specific salmonid in one specific region, demonstrating how a single geomagnetic cue might conceivably allow fish to navigate to their home rivers. It may not be possible to generalise this to Atlantic salmon, particularly to the return of adult fish to a variety of different European countries, where the magnetic isolines may not be as 'conveniently' located as they are on the west coast of North America.

2.4.1.4 Potential application of regional-scale models.

PTMs representing salmon at larger scales are likely to prove useful in two main contexts:

1. Modelling of outward migration of smolts from their rivers of origin, particularly on the east coast of Scotland, in order to determine the likelihood that they pass through wind farm sites, and to estimate the proportions of east and west coast fish that may pass through the Pentland Firth (or other areas of interest).
2. Modelling the return migration of adult fish from feeding grounds in the North Atlantic to establish probable arrival points of adult salmon in coastal waters, and therefore to estimate the proportions of these fish that pass through the Pentland Firth (or other areas of interest).

In the specific case of Scottish coastal waters, there is an alternative approach to estimating the number or proportions of salmon passing through areas of interest. This is only possible because of the existence of historical information derived from tagging and recaptures of salmon over the last 120 years. These data allow some consideration of potential salmon

movements around the coast, and provide a direct, data-driven, method of making some determination of the proportions of fish entering areas such as the Pentland Firth, and of separating this out at a catchment or river scale. This possibility is explored further in Chapter 5.

2.4.2 Modelling movements of salmon in coastal waters and extreme tidal environments

One particular weakness of large-scale hydrodynamic models is that they lack the resolution (spatial and temporal) to accurately represent the movement of water around complex coastlines, and therefore to resolve flows in extremely tidal areas. In order to model the trajectories of fish through such areas higher resolution models are required. These do not need to be of a fundamentally different type to larger scale models, but the actual models used, and the key forcings applied, are likely to be different. For instance, while many OGCMs and similar large scale studies make effective use of general purpose, open-access modelling frameworks and readily available public datasets, higher resolution modelling will most likely require site-specific models (with boundary conditions input from larger models) using proprietary or commercial code, and detailed local data such as accurate bathymetry and tidal flow measurements. Particle-tracking models, particularly those simulating actively swimming animals, are certainly much less common at this scale, and there are essentially no published studies on migratory salmon in this context. This represents a major gap in our ability to model the passage of fish, including migrating Atlantic salmon, through highly dynamic environments such as the Pentland Firth.

Fortunately, the requirements of the renewable energy industry (evaluation of available tidal and wave energy resources, selection of optimum sites for development, prediction of hydrodynamic stresses on infrastructure, and forecasting of potential changes in local hydrodynamics) mean that for some sites such high resolution models are already in place or under development, both by the academic and commercial sectors. These coastal systems are the focus of intense research activity, and understanding will increase (along with model accuracy) as the sector develops. However, much of this modelling work may currently be undertaken by developers and their contractors, and is therefore not readily available to researchers attempting to anticipate ecological implications. Re-tasking these existing models as the basis of particle-tracking simulations is likely to be the most cost-

effective approach, and may have additional applications (for example in the forecasting of risk from floating debris).

In constrained tidal channels (such as the Pentland Firth) tidal currents are likely to be the dominant influence on modelled particle trajectories. The influence of meteorological forcing is likely to vary, being perhaps less important in tidally dominated channels but more significant on open coasts. Of course, data on future meteorological conditions is not available, therefore probabilistic approaches may be required in order to anticipate the impact of wind forcings (Díaz et al. 2008).

2.4.2.1 Incorporating animal behaviour

The orientation mechanisms which are important during the open sea migration phase may become less important or even completely non-significant during the coastal migration stage, while other mechanisms may become significantly more important (Chapter 4). For instance, how fish behave in response to strong tidal flows will be very important, including any tendency to show behaviours that vary across the tidal cycle, such as selective tidal stream transport (STST), although so far there is no evidence of STST in salmon (Quinn et al. 1989). There is little published information concerning how salmonids respond to high flow speeds, and almost all of it refers to behaviour of smolts or juvenile fish in rivers. Smolts in rivers show a tendency to adopt a tail-first orientation when passing over weirs, may avoid regions of greatest flow acceleration (Kemp et al. 2008), and show rates of downstream passage which suggest that they may spend periods of time swimming against the current (Smith 1982). Brown trout also adopt a tail-first orientation when experiencing high flow acceleration (Russon & Kemp 2011). There is no evidence regarding similar responses to flow in the marine environment. In the absence of direct evidence concerning the behaviour of fish during transits of extreme tidal environments, IBM approaches might be used to explore the potential effect of different behaviours on movements through such environments.

2.4.2.2 Variability

The most important variation in higher resolution models of tidal waters is likely to be driven by tidal effects. Therefore simulation of a single spring-neap cycle could be adequate to capture most of the potential variability. However, depending on how important other

forcings are (particularly wind and wave effects), it may be necessary to run simulations accounting for a variety of different meteorological conditions (for example, repeat model runs could be run with predominantly westerly or easterly winds). Additional simulations could be run to determine the outcome of extreme events. Again, accounting for this variation is already of interest to the academic and industry sectors, so existing model runs including different values of meteorological variables may be available.

Timing of release of particles (for example release at different points in the tidal cycle) into hydrodynamic simulations can have significant effects on their trajectories (Hays et al. 2010). Particle tracking models allow easy exploration of the effect of varying timing of entry. Similarly, the point of entry into such a system will also influence trajectories (Adlandsvik et al. 2004). At this point, it is not known how far from the coast fish are as they transit the Pentland Firth. Even within the scale of a few tens of metres, differences in location will influence trajectories.

2.4.2.3 Advantages to high resolution particle tracking approach

In summary, this type of approach has several advantages for estimating the likelihood of passage through development locations, particularly in the case of the Pentland Firth:

1. **A range of underlying hydrodynamic models may already be available.** The renewable energy industry, along with the academic community, already has need for (and interest in) models of these environments. It should be possible to use existing models rather than having to build new ones 'from the ground up' for PTMs.
2. **Modelling would allow exploration of the effects of different behaviours on rates of passage through proposed development sites.** In the absence of empirical data on how migratory salmonids behave while transiting extreme tidal environments, PTMs can allow exploration of the effects of different (biologically realistic) behavioural strategies.
3. **Modelling allows exploration of the effects of entering tidal locations at different points in the tidal cycle.** It is likely that fish will enter regions such as the Pentland Firth at a number of different tidal states, and modelling allows the effect of these timing differences to be explored.
4. **Modelling allows consideration of the effects of variation in environmental conditions.** Multiple simulations can be run under a range of different meteorological conditions to explore how this may affect fish trajectories.

5. **Modelling may allow the impact of hydrodynamic changes resulting from turbine operation to be predicted.** The presence of structures will alter hydrodynamics, and the operation of tidal energy devices will cause further changes. This will change the conditions experienced by passive or active particles, and this can be explicitly considered using hydrodynamic models
6. **The approach has potential to generate hypotheses for testing in the field.** Currently our knowledge of the behaviour of salmonids in Scottish coastal waters is lacking. In addition to allowing us to explore the effects of various factors (such as fish behaviours) on model outcomes, particle tracking simulations could identify key hypotheses that would need to be tested to validate behavioural assumptions.

2.5 Recommendations for advancing PTMs for salmon

In order to develop particle tracking models to improve our understanding of salmon migration around Scotland, three activities are suggested:

A. Implementation of a high resolution particle-tracking model for the Pentland Firth. A demonstration of such a model is provided in Chapter 3. Once the approach has been successfully applied to the Pentland Firth, similar models could be adapted for application to other sites.
B. Implementation of a larger-scale particle-tracking model covering near-coastal areas of the North Sea and the North Atlantic, in order to simulate outward migration of post-smolts and return migration of adult salmon through Scottish coastal waters.
C. Collection of empirical data to support the above modelling activities.

2.5.1 Activity A - High resolution modelling of salmon passage through the Pentland Firth

- **A high resolution particle-tracking model (PTM) could be implemented off-line using outputs from an existing hydrodynamic model of the Pentland Firth.** This avoids the costs associated with establishing and validating a completely new hydrodynamic model. The following models are therefore recommended on the basis that they are known to have been applied (or are in the process of being applied) to the Pentland Firth:
    - POM (see Chapter 3)
    - MIKE (Easton et al. 2012)
    - SUNTANS (Baston & Harris 2011)
    - TELEMAC
    - DELFT3D

  Of these, the unstructured grids used by MIKE, TELEMAC and SUNTANS may offer the best capability for simulating the detailed flow conditions of the Pentland Firth. However, only POM has been trialled for simulating actively swimming particles in this context. As an additional consideration, TELEMAC, SUNTANS and POM are available on an open-source basis.

- **A 2-dimensional implementation could be sufficient**, since these waters may be considered 'well-mixed', and migrating salmon may be mostly swimming close to the surface in coastal waters. However, this could be reconsidered in the light of any contradictory evidence.
- **An initial implementation could concentrate on only tidal and topographical forcing through the Pentland Firth,** since these are likely to be by far the dominant forcings. However, attention should be paid to ongoing research on the influence of wind and wave forcings in the Pentland Firth, and when possible these should be incorporated into a PTM, to simulate the effects of a range of potential conditions.
- **Recommended best practice for PTMs should be followed where possible** (Brickman et al. 2009), including**:**
    - Use of **RK4 integration** (or equivalent) for particle advection
    - Incorporation of **random walk displacement** to account for sub-grid scale processes, using the Visser (1997) correction
    - Simulation of **sufficiently large numbers of particles** (Simons et al. 2013)
- **Active motion of migrating fish should be incorporated using a correlated random walk**, which can be modified to include orientation behaviour based on insights from existing knowledge (Chapter 4) or on new information arising from future empirical studies.
- **Individual particles should also be given effective 'land avoidance' behaviours** based on reflection from land, preferably with a random component.
- **Sensitivity analyses should be conducted to assess the effect of variations in model conditions, such as:**
    - Timing of particle release into tidal systems
    - Location of release into tidal systems
- **Proposed renewable energy arrays could be explicitly simulated within a model as 'Lagrangian targets' where impact assessment is the primary goal,** so that encounters between modelled particles and arrays can be enumerated.

2.5.2 Activity B - Larger scale modelling of Atlantic salmon migration

- **The most promising model system is likely to be the Regional Ocean Modelling System** (ROMS) on the basis of its flexibility and track-record of use for simulating Atlantic salmon migration (e.g. Mork et al. 2012).
- **General particle-tracking and active movement recommendations should be followed as in Section 2.5.1 above**
- **Outward migration of smolts could be simulated** with a range of start points (corresponding to major salmon rivers), with particular emphasis on the east coast of Scotland.

2.5.3 Activity C - Empirical studies to support modelling

2.5.3.1 Model validation

For the Pentland Firth (and other highly energetic tidal channels) there is currently insufficient data for model validation (Easton et al. 2012), and validation of models in extreme tidal environments is in any case not straightforward; differences between modelled and measured currents are often greatest in areas of highest flow (Kuang et al. 2012). However, validation of hydrodynamic models is a general priority for many aspects of marine renewable energy and the environment, therefore collection of additional data for validation of underlying hydrodynamic models is not recommended here as a *specific* priority for advancing PTMs. Any data that is generated for other purposes will be beneficial.

Nevertheless, **it is recommended that small-scale drifter experiments are carried out within the Pentland Firth**, to validate particle drift simulations. No data from previous drifter experiments appear to be available from any studies carried out in the Pentland Firth to compare with model outputs. Large numbers of drifter runs might be required, though low cost methods could be explored, since drifter runs are likely to be of much shorter duration (hours) compared with large-scale drifter experiments.

2.5.3.2 Salmon behaviour

Empirical observations on the behaviour of salmon within coastal waters are needed in order to parameterise PTMs. Some of the required information can be derived (at least on a provisional basis) from existing knowledge (see Chapter 4), however there are many knowledge gaps, including (but not limited to):

- Swimming depths
- Responses to high flows in the marine environment
- Orientation on the basis of environmental cues

Collecting data to address these knowledge gaps is likely to require tagging, tracking and telemetry studies. However, while the technologies used for such studies are well-established, they are yet to be applied in such challenging conditions as the Pentland Firth, and innovative approaches and new methods are likely to be required. Until such data are available, modelling of salmon migration will be reliant on assumptions concerning salmon behaviour.

Chapter 3. Demonstration of a PTM for the Pentland Firth

In order to illustrate the possible use of high resolution hydrodynamic models to assess the probability of salmon entering renewable energy array locations (as discussed in Chapter 2), a basic particle-tracking model of the Pentland Firth and Orkney Waters (PFOW) has been implemented. For this initial demonstration, west to east movement through the Pentland Firth was considered, representing the return migration of adult salmon (towards east coast rivers) along the north coast of Scotland and into the North Sea. It should be noted from the outset that the purpose of this model implementation is to illustrate one potential application of this approach, not to act as an actual impact assessment for migrating salmon**. As such, any outputs from the model are merely representative of the type of output that could be obtained from a full implementation, and are not intended to be read as statements about absolute or relative passage rates through real array locations.**

3.1 Model setup

3.1.1 Hydrodynamic model

A 2D formulation of the Princeton Ocean Model (POM) was set up to encompass the PFOW area. POM is a widely used modelling framework, and has been adapted for applications at a wide range of spatial scales, in a wide range of locations, for a wide range of scientific problems (Table 2.1) including particle-tracking approaches to study the migration of salmonids (Bourque et al. 1999). The model domain in this case extends from 4°45´W to 2°W and from 57°30´N to 60°N (Figure 3.1). A structured grid was used to represent the domain, with a spatial resolution varying from >1km at the boundaries to <200m within the Pentland Firth. Bathymetry for the model was obtained from Admiralty data.[5]

Lateral boundary conditions were taken from a shelf-model (domain Iceland-Britanny-Norway) which was written as a surge model, driven at the open boundaries by elevations taken from global tidal models (TPX07, NAO99 and related constituents) and direct tidal forcing. This tidal model has been calibrated against UK Class A tide gauge data, generally with errors of 10cm in astronomical tide and 15cm in surge elevations. Prior to beginning the particle tracking exercise, the model was 'spun up' for 48hrs.

[5] http://www.seazone.com

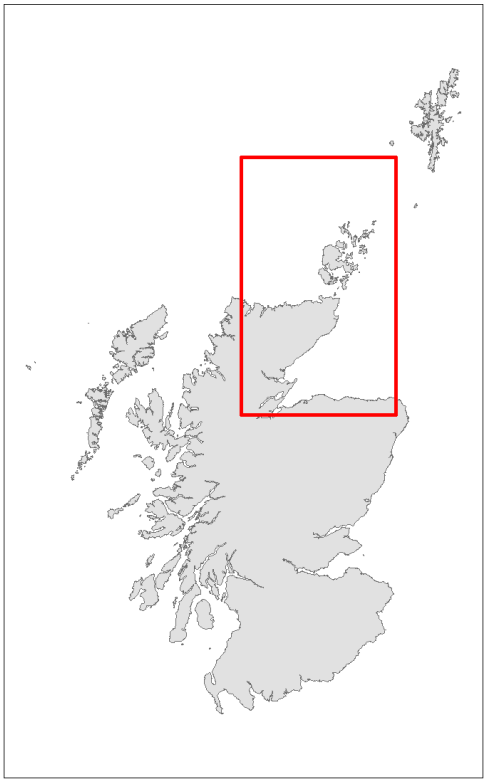


Figure 3.1 Spatial context of modelling study
(red box indicates domain of the hydrodynamic model).

3.1.2 Particle tracking

Particles were released in 10 x 10 km boxes centred on a latitude and longitude specified by the user. Each release consisted of 3480 particles. All simulations were initiated at the start of the flood tide (which runs west to east through the Pentland Firth) and tracer positions were recorded hourly for 143 hours. A simple land-avoidance strategy was coded into the model; when particles encounter the coast they make a 90° turn to the left. For this initial exploration of the model, five different simple movement strategies were investigated:

1. Passive advection with the current
2. Active swimming on a fixed bearing of 135° (heading south-east):
    a. at constant speed of 0.1 $m.s^{-1}$
    b. at constant speed of 0.3 $m.s^{-1}$
    c. at constant speed of 1.0 $m.s^{-1}$
3. Active swimming on a fixed bearing of 90° (heading east) at 0.2 $m.s^{-1}$

For each of these strategies, two simulations were run, one with a particle release centred on 58.7°N, 3.5°W and one centred on 58.8°N, 3.5°W. Particle trajectories were analysed in MATLAB. In addition to displaying the trajectories of particles, the cumulative number of

particles passing further south than 58.2°N, or further east than 2.5°W was recorded and assumed to indicate successful (eastwards) passage through the Pentland Firth.

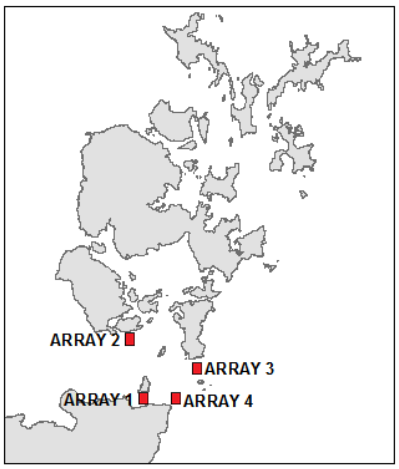


Figure 3.2 Locations of simulated arrays, based on proposed locations for four tidal energy developments. Arrays were simulated as simple linear 'fences' of devices and did not approximate the spatial configuration of any leasing areas or proposed arrays.

3.1.3 Tidal arrays

Four tidal energy arrays were simulated as simple linear 'fences' (single rows of devices). These hypothetical arrays were placed in locations near to the locations of the four Crown Estate leasing areas (see Appendix) for tidal energy development in the Pentland Firth (Figure 3.2). They were not intended to represent the exact locations or configurations of any real proposed arrays, merely to allow for some exploration of the type of outputs that could be generated by this type of model. No effects of arrays on local hydrodynamics were simulated. Arrays were treated as 'Lagrangian targets' (Section 2.2.2); A MATLAB script was used to identify and record all instances where particles encountered one of the arrays (any time where the interpolated trajectory of the particle intersected the location of a device in one of the arrays). Particles were sometimes recorded as encountering a single array many times over the course of several minutes; these were not considered to represent separate encounters and therefore any such multiple encounters within a 0.1 hr (6 minute) period, were considered to represent a single encounter. No attempt is made here to model actual interactions between particles and arrays; the purpose of this exercise is merely to explore how this type of model could be used to forecast the rate at which fish passing through the Pentland Firth might encounter the location of a proposed array. The model did not consider interactions and all particles passed through array locations unhindered.

3.2 Model Output

3.2.1 Movement of particles through the Pentland Firth

Passive particles, advected by the tidal flows in the model, were predominantly moved back-and-forth within the Pentland Firth. However, as a result of a small residual eastwards current, even some passive particles passed across the target lines (58.2°N or 2.5°W), though less than 30% had reached this point by the end of the model run (Figure 3.3A). Successful passage through the Pentland Firth did not appear to be substantially affected by whether the particles were released from a box centred on 58.7°N or 58.8°N (Figure 3.3A). Example trajectories (Figs. 3.4.A,B) illustrate passively drifting objects making multiple passages through the Pentland Firth.

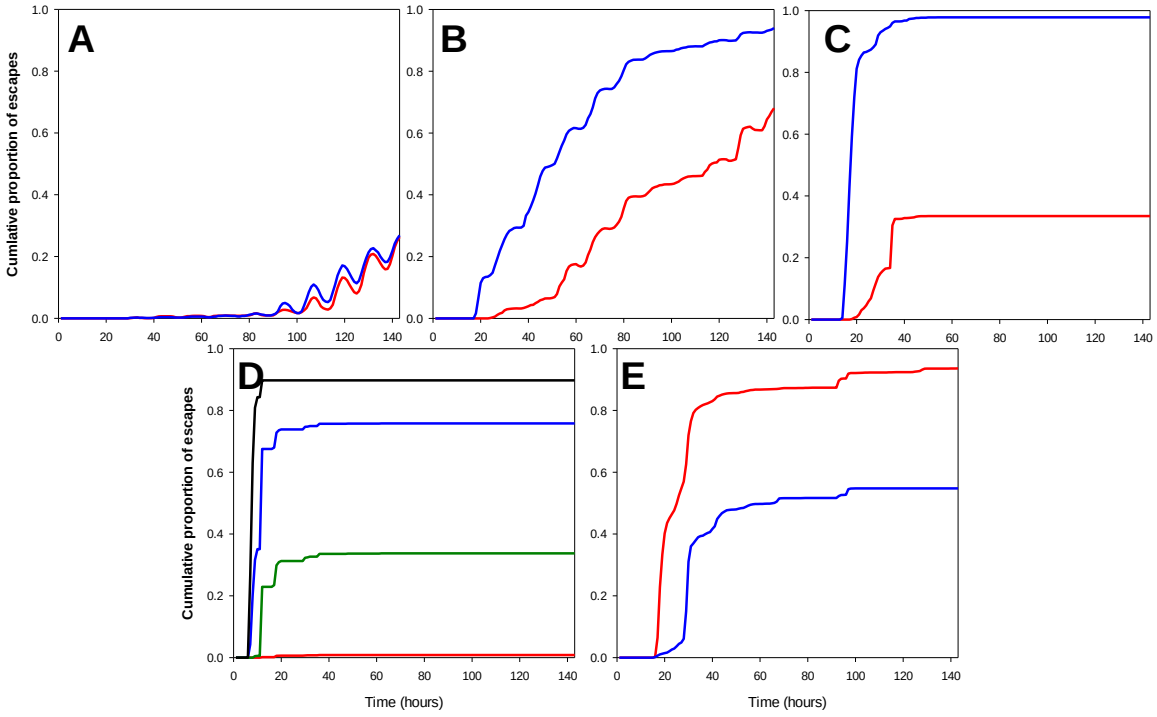


Figure 3.3 Plots of cumulative successful particle transits through the Pentland Firth (success defined as passing to the south of 58.2°N, or to the east of 2.5°W), with five different movement strategies (A – passive advection; B – fixed vector SE at 0.1 m.s^{-1}; C - fixed vector SE at 0.3 m.s^{-1}; D - fixed vector SE at 1.0 m.s^{-1}; E - fixed vector E at 0.2 m.s^{-1}) after releases from different latitudes (Red - 58.7°N, Blue - 58.8°N, Green - 58.75°N, Black - 58.85°N).

Adding a modest amount of consistent directional movement to each particle (heading southeast with a 'swimming' speed of 0.1 m.s^{-1}) greatly increased the proportions of particles successfully transiting the Pentland Firth, particularly for the release at 58.8°N - over 90% of the particles made a successful transit by the end of that simulation (Fig. 3.3B).

Tidal influences were still significant; at the end of the simulation run some particles still remained to the west of the Pentland Firth (Fig 3.5B). However, it should be noted that the cumulative escapes plots (Fig 3.3B) had not reached a definite asymptote by the end of the simulation and therefore more successful transits are likely to occur with a longer model run.

Similarly, when particles were moving actively to the east at 0.2 $m.s^{-1}$, they also showed a relatively high proportion of successful transits within the available time, except in this case the 58.7°N release position led to the greatest proportion of escapes (Fig 3.3E). While less than 60% of particles released from 58.8°N escaped, it is not certain that an asymptote had been reached, so further escapes may occur in a longer simulation. However, it is evident that some particles did become 'stuck' on the coast in this simulation (Fig 3.5E).

Increasing the speed of south-easterly moving particles led to an increase in the number of particles that appeared to be getting 'stuck' on the coast. Particularly for releases from 58.7°N, and at the highest speed (1.0 $m.s^{-1}$), the number of particles successfully passing through the Pentland Firth was much lower than for other scenarios, with a large proportion of particles apparently becoming 'stuck' on the coast (Fig. 3.3D, red line). As a result of the disappointing performance of this particular simulation, additional simulations were run for 1.0 $m.s^{-1}$, tracking particles released at 58.75°N and 58.85°N. In all cases with faster moving particles, numbers of escaping particles seemed to reach asymptote within this time (48 hrs) suggesting no benefit of longer simulation runs, and that any particles remaining within the model domain were irreversibly stuck at the coasts. As would be expected, trajectories of particles moving at the faster speeds were generally much more direct (excluding those which ended on the coasts), carrying them through the Pentland Firth efficiently (Figs. 3.4E and F). Releases of SE-moving particles from higher latitudes led to more successful transits, with (for example) almost 100% of particles moving at 0.3 $m.s^{-1}$ passing the boundary in less than 48 hrs when released from 58.8°N (Fig 3.3C).

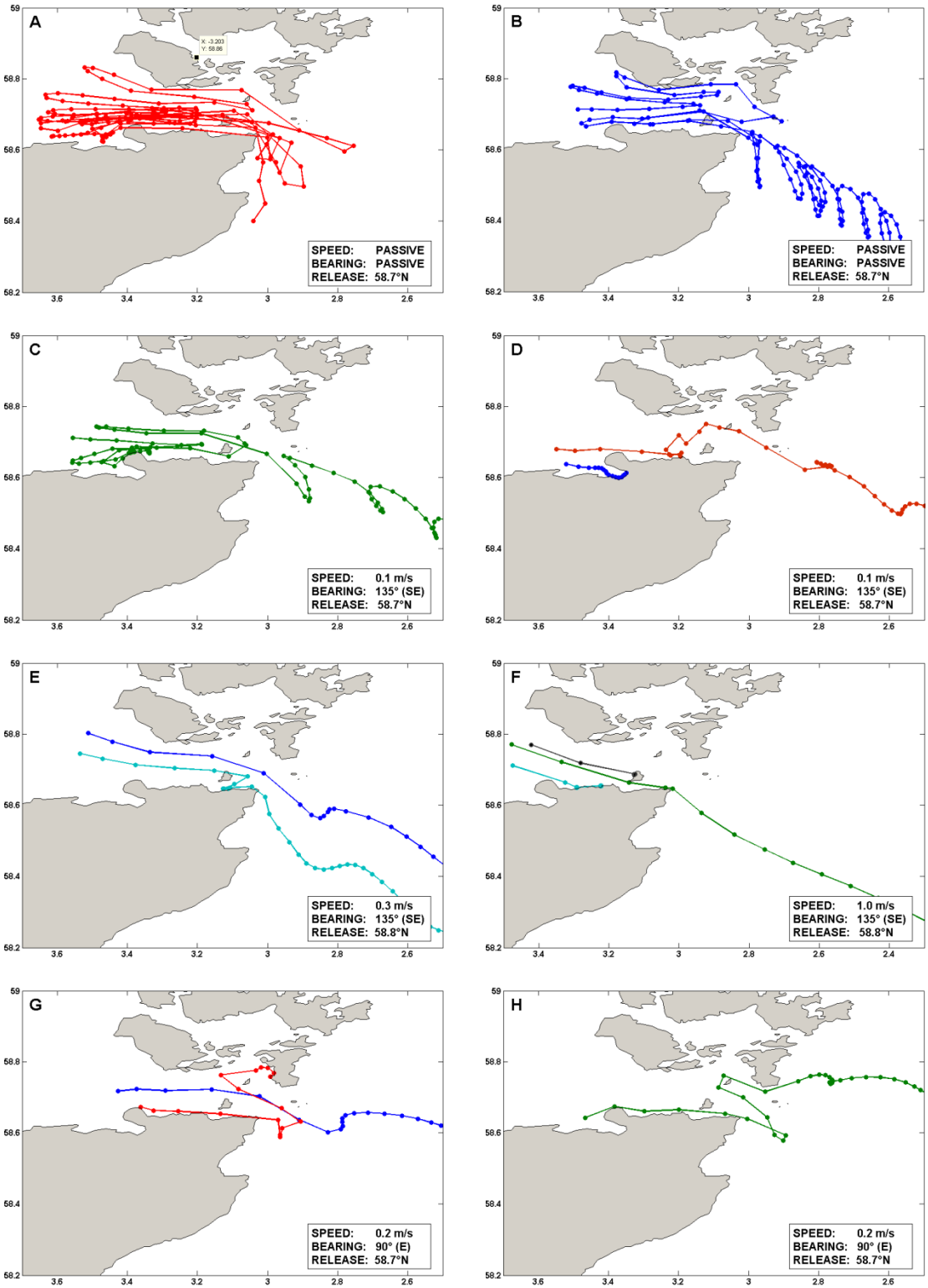


Figure 3.4 Example trajectories from a particle-tracking model of the Pentland Firth. All particles were released at the start of the flood tide and the simulation was run for 143 hours. Markers indicate hourly recorded particle positions; lines between markers are interpolated and do not necessarily represent actual pathways taken by particles in the model. Lines and markers are coloured to allow trajectories of individual particles to be distinguished, but colours have no other significance.

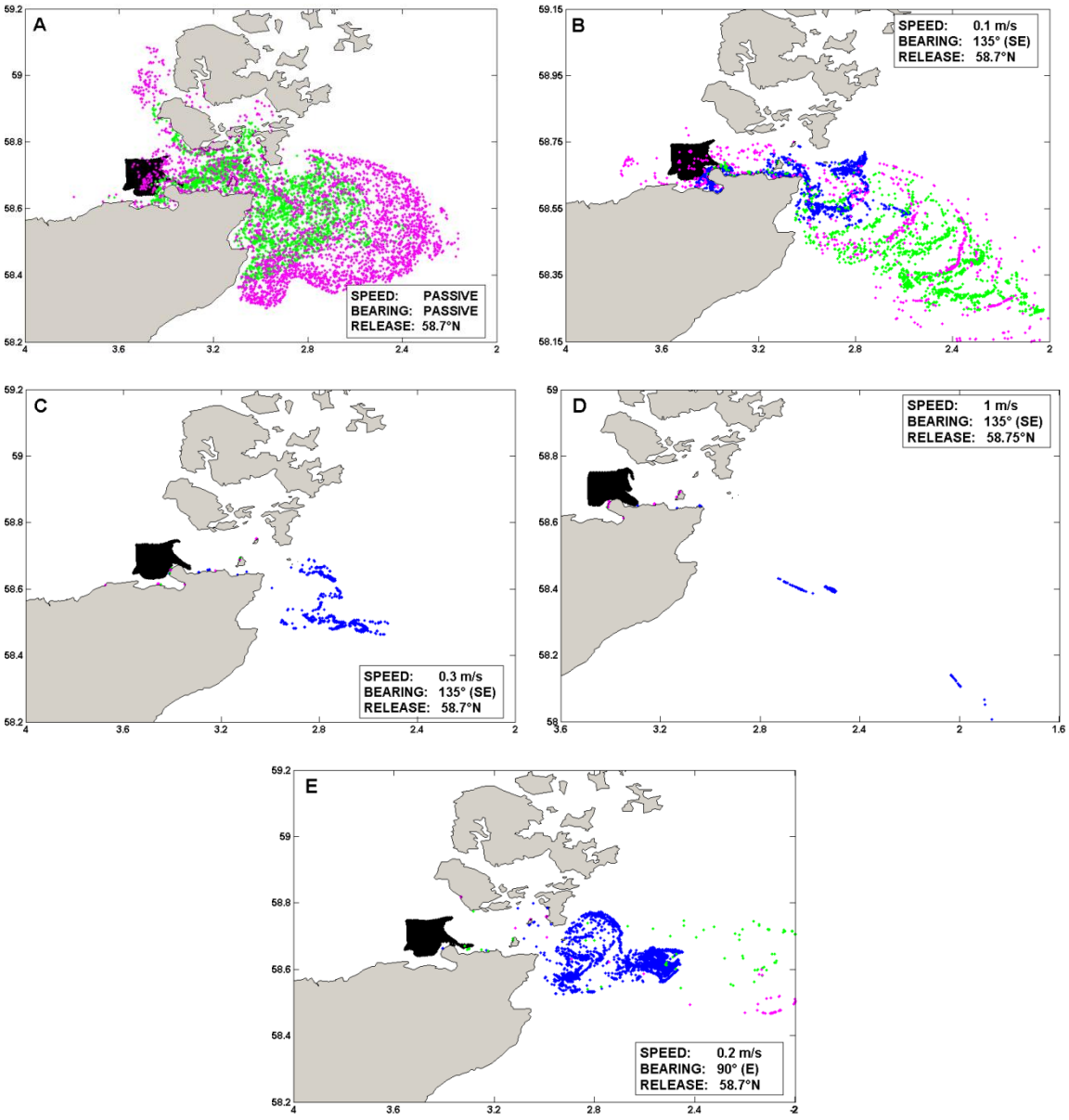


Figure 3.5 Dispersion of particles through the Pentland Firth following release at start of flood tide, illustrating the effect of 5 different movement strategies: **A** – passive advection; **B** – fixed vector SE at 0.1 m.s^{-1}; **C** - fixed vector SE at 0.3 m.s^{-1}; **D** - fixed vector SE at 1.0 m.s^{-1}; **E** - fixed vector E at 0.2 m.s^{-1}. Coloured symbols indicate positions of individual particles at different times within the simulation: Black - shortly after the start of the simulation; Blue - 16 hours; Green - 72 hours; Pink symbols – 143 hours. 16 hr (Blue) positions omitted from the plot of passive advection for clarity. Note that in D, as a result of the high swimming speed, the majority of particles have either passed outside of the model domain or become stuck on the coasts within 16 hours of the simulation start.

3.2.2 Hypothetical array encounters[6]

The number of encounters between particles and hypothetical arrays varied between simulations, as a result of differences in several factors. In addition to affecting the number

[6] An 'encounter' in this context refers simply to the passage of a particle through the location of an array. Such encounters are not presumed to have any impact on particles (Section 3.1.3)

of encounters, altering the simulation parameters sometimes affected the proportion of particles encountering arrays multiple times and the relative numbers of particles entering each of the four array areas.

Table 3.1 Summary of array encounter data for particles released under several scenarios. P = Particles (total number of particles which encountered arrays). E = Encounters (total number of particle-array encounters).

Swimming Direction	Swimming Speed ($m.s^{-1}$)	Release Latitude (°N)*	Array encounters									
			Array 1		Array 2		Array 3		Array 4		TOTAL	
			P	E	P	E	P	E	P	E	P	E
Passive	0 (passive)	58.7	918	1245	1515	2652	687	878	1781	2976	2873	7751
Passive	0 (passive)	58.8	461	579	2715	5240	749	1041	1426	2296	3067	9156
135° (SE)	0.1	58.7	1021	1293	51	55	235	243	1353	1925	1901	3516
135° (SE)	0.1	58.8	403	475	829	872	197	217	623	842	1582	2406
135° (SE)	0.3	58.7	543	612	0	0	36	36	272	281	781	929
135° (SE)	0.3	58.8	10	11	103	103	6	6	360	391	472	511
135° (SE)	1.0	58.75	442	442	0	0	0	0	280	631	722	1073
135° (SE)	1.0	58.8	602	602	0	0	0	0	795	1053	1397	1655
135° (SE)	1.0	58.85	77	77	0	0	0	0	907	907	984	984
90° (E)	0.2	58.7	476	541	87	96	225	276	707	715	1291	1628
90° (E)	0.2	58.8	21	21	1582	1754	671	848	140	140	1900	2763

*Particles were tracked from 10x10km boxes centred on the listed latitude (all releases were centred on a longitude of 3.5°W).

3.2.2.1 Array 1

Fewer than 1100 particles (30% of the 3480 particles released) encountered Array 1, regardless of release location and particle behaviour, and less than 10% encountered the array more than once (Table 3.1; Fig. 3.6C). Particles released nearer to the coast of mainland Scotland passed through this array location in greater numbers than when they were released further north (at 58.8°N), especially when the particles were also actively swimming on an easterly bearing; less than 1% of east-swimming particles released at 58.8°N passed through the array.

Active particle swimming generally led to a smaller number of passages through this array, and to smaller proportions of particles passing the array multiple times, relative to entirely passively drifting particles. The only exception to this was that when particles were released at 58.7°N with active swimming to the south-east at 0.1 $m.s^{-1}$, a slightly greater number of particles passed through the array than in the passive drifting scenario (1021 compared to 918). At the fastest swimming speed (1.0 $m.s^{-1}$ to the south-east) no particles encountered the array more than once.

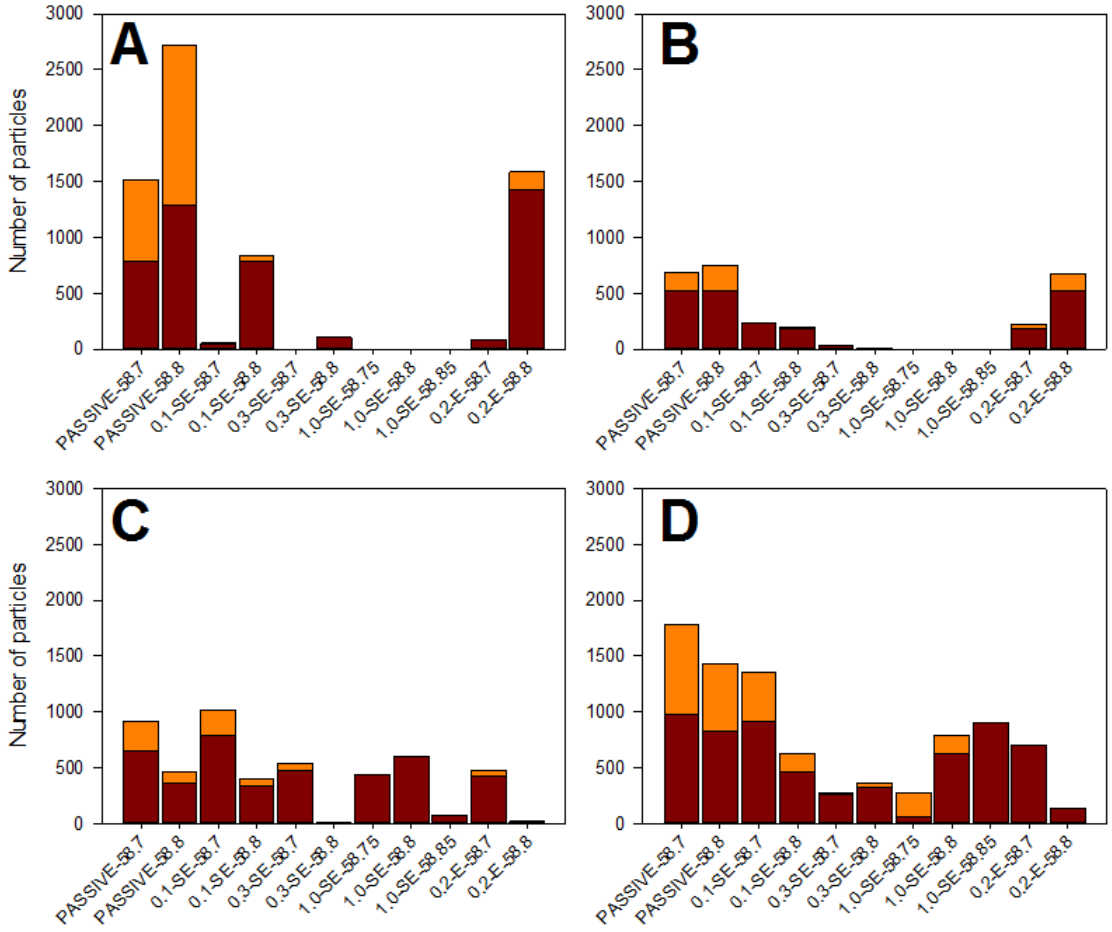


Figure 3.6 Number of particles encountering each of four hypothetical tidal arrays within the Pentland Firth during a 143-hour particle tracking simulation. Red portions of bars indicate numbers of particles experiencing a single transit of the array, orange portions indicate number of particles which experienced multiple array passages. Bar titles give particle speed (passive, 0.1 $m.s^{-1}$, 0.2 $m.s^{-1}$, 0.3 $m.s^{-1}$ or 1.0 $m.s^{-1}$), particle heading (SE – south-east; E – east) and latitude of release (decimal degrees N). **A –** Array 2; **B** – Array 3; **C** – Array 1; **D** – Array 4.

3.2.2.2 Array 2

A relatively large proportion (up to 78%) of passive particles passed through Array 2, especially when those particles were released at 58.8°N (Fig 3.6A). Regardless of release location, around 50% of passive particles which encountered the array did so more than once. However, any active south-easterly movement of particles drastically reduced the number of particles encountering the array and resulted in zero (or close to zero) particles encountering the array more than once (Fig. 3.6A). Furthermore, releases from the more southerly position (58.7°N) led to fewer than 100 encounters, except in the case of entirely

passive particles. When released from the more northerly position, eastward-swimming particles encountered this array in relatively large numbers (45% of particles).

3.2.2.3 Array 3

Fewer passive particles encountered this array compared to the other three arrays (Fig. 3.6B), the largest number of encounters being 749 (when passive particles were released at 58.8°N), and the number of particles experiencing multiple encounters was always less than 10%. Any south-easterly swimming behaviour reduced the number of encounters, with fast swimming of 1.0 $m.s^{-1}$ to the south-east leading to no encounters taking place. Generally, release location had little effect on the model outcomes, except when particles swam on an easterly heading; in which case number of encounters was greatest for particles released at 58.8°N (19% - close to the value for passive particles).

3.2.2.4 Array 4

In most cases, larger numbers of particles encountered this array than any of the others (Fig. 3.6D), the only exceptions being passive particles released at 58.8°N, south-easterly swimming particles moving 0.1 $m.s^{-1}$ from 58.8°N, easterly swimming particles moving at 0.2 $m.s^{-1}$ from 58.8°N (which all encountered Array 2 in greater numbers) and south-easterly heading particles moving 0.3 $m.s^{-1}$ at 58.7°N (which encountered Array 1 in greater numbers). These results would seem to indicate that large numbers of particles, in most scenarios, are channelled through the fast-moving waters off Duncansby Head.

3.2.3 Cumulative encounters

This approach can be extended to examine the combined number of encounters with all four arrays. While the overall number of array encounters in a scenario involving multiple arrays is the sum of the numbers of encounters involving the individual arrays, the numbers of particles involved in those encounters does not rise in the same way. For example (see Table 3.1), after release from 58.8°N, 2715 passive particles had a total of 5240 encounters with Array 2 (a mean number of encounters , including all 3480 particles in the simulation, of 1.51 encounters per particle). Adding in the other three arrays causes the number of encounters to rise to 9156 (almost double) while the number of particles involved in those interactions only rises to 3067 (a mean number of encounters of 2.63 encounters per particle). This is accounted for by an increase in the number of particles making multiple

passes through single arrays, or encountering multiple arrays (Fig. 3.7). As with the single-array results, active particle motion reduced the total number of particle-array encounters, and in this case it also reduced the proportion of particles experiencing multiple encounters.

For all scenarios (Fig. 3.8), numbers of encounters were not uniformly distributed across the four arrays (G-Test, $p < 0.01$ for all combinations of speed, bearing and release latitude). As would be expected from the individual array results, the proportions of particles encountering the different arrays were affected by the swimming speed and direction of the particles, and the release latitude (Fig. 3.8). Higher latitude releases led to proportionately greater numbers of encounters with the more northerly arrays (Arrays 2 and 3), while releases further south and south-easterly swimming behaviour increased the proportion of encounters involving the arrays on the south side of the Pentland Firth (Arrays 1 and 4).

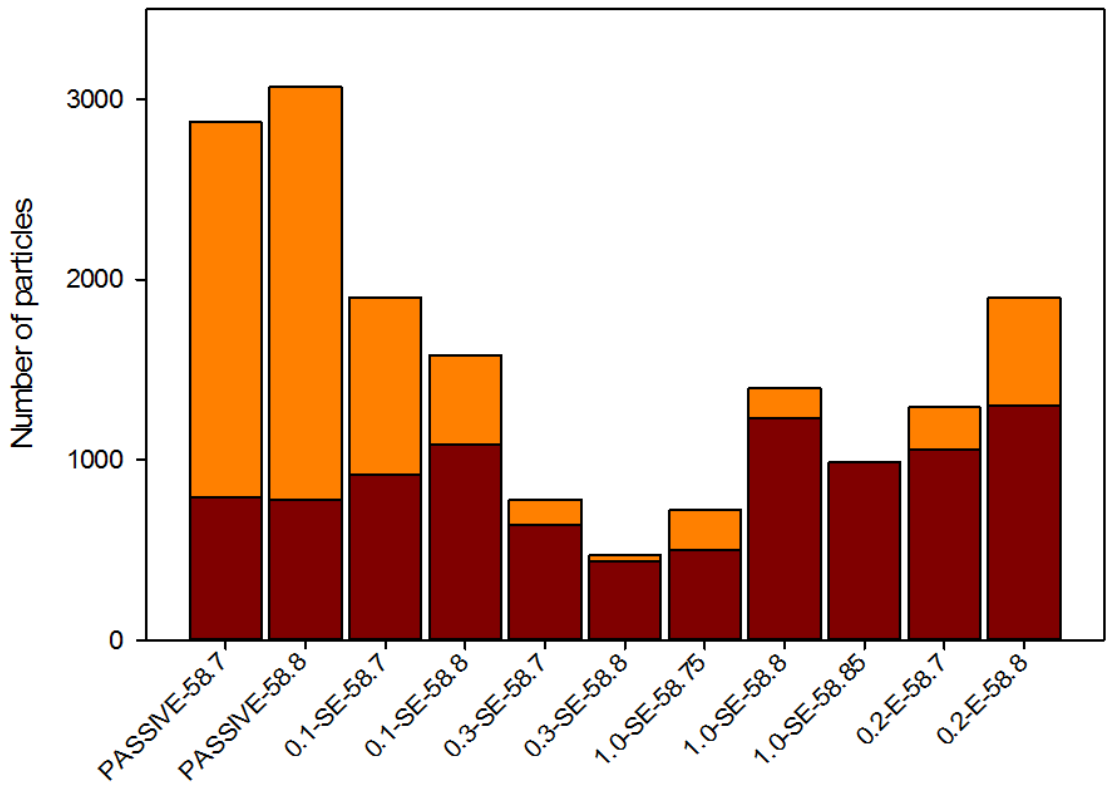


Figure 3.7 Number of particles encountering all four hypothetical tidal arrays during a 143-hour particle tracking simulation. Red portions of bars indicate numbers of particles experiencing a single transit of one array, orange portions indicate number of particles which experienced multiple array passages, either through the same array or through multiple different arrays. Bar titles indicate particle speed (passive, 0.1 $m.s^{-1}$, 0.2 $m.s^{-1}$, 0.3 $m.s^{-1}$ or 1.0 $m.s^{-1}$), particle heading (SE – south-east; E – east) and latitude of release (decimal degrees N).

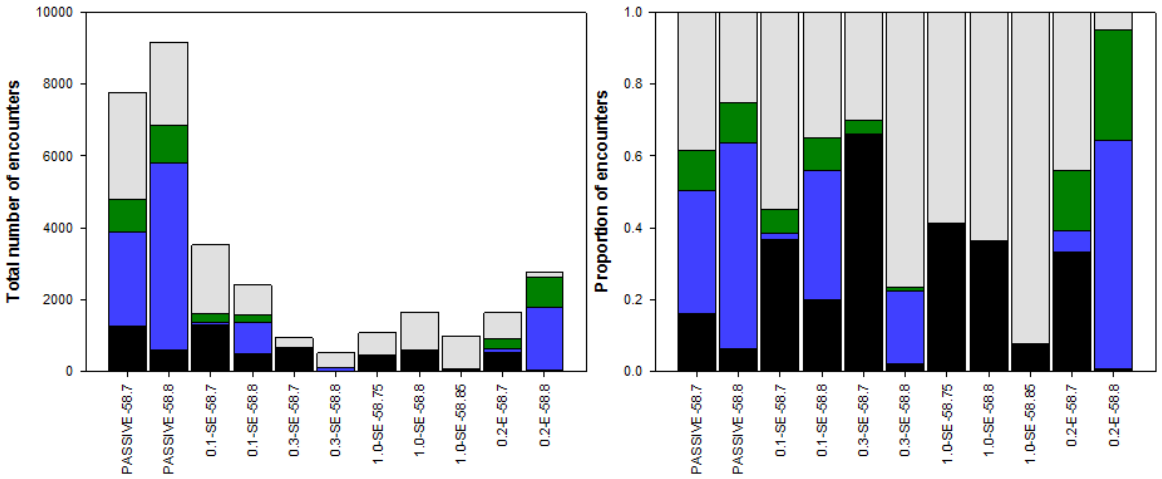


Figure 3.8 Encounters between particles and arrays during 143-hour particle tracking simulations with different model parameters. **Left figure**: Absolute numbers of encounters involving the four arrays. **Right figure**: Proportions of total encounters involving each of the four arrays. Colour coding: **Black –** Array 1; **Blue** – Array 2; **Green** – Array 3; **Grey** – Array 4. Bar titles indicate particle speed (passive, 0.1 $m.s^{-1}$, 0.2 $m.s^{-1}$, 0.3 $m.s^{-1}$ or 1.0 $m.s^{-1}$), particle heading (SE – south-east; E – east) and latitude of release (decimal degrees N).

3.3 Discussion

At this stage, the modelling that has been carried out is intended simply to illustrate the application of a PTM approach, not to act as a source of information on migratory fish encounter risk in the Pentland Firth. Nevertheless, it is still possible to draw some preliminary conclusions:

1. The point of entry into the Pentland Firth (particularly in terms of latitude, or distance from the north coast of the Scottish mainland) affects the likelihood of encounter with arrays at different specific sites.
2. Any active swimming behaviour reduces the overall number of particle-array encounters and the proportion of particles which encounter arrays multiple times. This is an important point, since it suggests that the number of encounters involving actively moving animals with arrays could potentially be much lower than those expected under a passive drifting scenario. Any tendency of particles to move to the south (for example while moving on a south-easterly bearing) reduces encounters with arrays on the Orkney side of the Pentland Firth, while increasing encounters on the south side of the firth.
3. The hydrodynamics of the Pentland Firth may lead to substantial differences in the potential rates of encounters between migratory fish and specific marine renewable energy arrays. These differences will also be strongly dependent on the behaviour of the fish as they transit these areas.

The outputs from this modelling approach show that it is possible (and relatively simple) to use hydrodynamic models to produce information on the probability of migrating salmonids passing through defined sites within the Pentland Firth, by representing those sites as Lagrangian targets. It can be used to estimate the relative number of potential encounters with arrays positioned in a variety of locations, and to establish the cumulative encounter rate where there are likely to be multiple arrays. It can account for the potentially substantial (and life-stage dependent) influence of extreme hydrodynamics, and allows a number of potential variables (such as release location and swimming behaviour) to be easily explored. However, the implementation presented here is an early-stage model and a number of simplifications and assumptions have been made. Several enhancements and appropriate biological data would be required before this technique could be applied in a rigorous manner.

1. While the model grid used here did allow for somewhat variable resolution, the overall resolution was relatively low (maximum resolution was 200m) and in general fluid flows around more complex coastlines are modelled better using unstructured grids (Section 2.1.1). The accuracy of the model may therefore be improved by the use of a modelling framework such as MIKE, TELEMAC, SUNTANS, or DELFT3D, which allow for unstructured grids and have previously been applied to the Pentland Firth.
2. The bathymetry data obtained from Admiralty datasets for this simulation, were relatively low resolution. More detailed bathymetry data have been collected by Marine Scotland Science[7] and by individual developers, and the best available data should be used for future PTM work.
3. Values of some parameters were chosen on an arbitrary basis for demonstration purposes, and sensitivity analyses should be carried out to explore the response of the model to changes in these parameters. For example, conclusions from particle modelling can be very sensitive to the numbers of particles released (Simons et al. 2013). In this case 3480 particles were used, but this choice was arbitrary and constrained by the underlying particle tracking framework of this model. Future simulations could aim to explore the impacts of particle number in order to determine the optimal quantity.
4. The behaviour of 'fish' in the model is critical to the model outcome, and fish behaviours incorporated in this model covered a range of conjectural and arbitrary possibilities. To reduce uncertainties, it is important that more realistic behaviours are incorporated in future models; these should ideally be based on empirical data on fish behaviour. In particular:

[7] http://www.scotland.gov.uk/Topics/marine/science/MSInteractive/datatype/Bathymetry/data/PentlandFirthBathymetry

   a. The land-avoidance method implemented in the model should be improved. A number of actively moving particles became 'stuck' on coastal features (see Figs. 3.4D, F and G); for example, some particles could not escape Dunnet Bay. This is clearly not biologically realistic.
   b. Fixed vector swimming (as modelled here for actively moving particles) is unlikely to be a biologically realistic behaviour for coastally migrating salmon. Even if fish are subsequently found to approximate fixed vector swimming in the wild, their ability to maintain a fully consistent vector will be limited. Future modelling should introduce 'noise' into migratory fish movement, for example by adding probabilistic variation to swimming vectors at each time step (using a correlated random walk) or by restricting active orientation to a subset of individual time steps. Furthermore, orientation behaviour may change spatially and temporally as salmon approach the vicinity of their home river.
   c. While this simulation incorporated orientation to particular directions, and accounted for the effect of flow on passive or oriented particles, it did not account for any responses to flow itself. Salmonids may respond to changes in flow, for example by avoiding regions of greatest acceleration (Kemp et al. 2008).
5. Tidal energy arrays were simulated as simple linear arrays of devices. While their positions approximated those of four proposed tidal arrays in the Pentland Firth, they do not accurately represent the shape and extent of the real arrays that may be deployed in these locations. A future model implementation should at minimum use the shape of the leasing areas or, where available, more accurate information about actual configurations of renewable energy arrays.
6. Meteorological forcing may (or may not) play a substantial role in fish trajectories. Considerable anecdotal accounts by fishers indicate that onshore winds increase catches in coastal netting stations (Menzies 1937), while offshore winds reduce them, suggesting that the positions of salmon relative to the shore are affected by wind. This may affect the numbers of fish that may potentially encounter arrays during their migration.

Finally, it is important to emphasise that this approach is not intended to act on its own as a method of assessing risk to migratory fish – it is only Stage 2 (Section 1.3) of a three stage process. It must be coupled at one end to larger scale data (for example, in the case of the Pentland Firth, data on numbers of fish passing through the Firth itself rather than using other routes into the North Sea) and at the other end to data on the nature of any interactions between devices and fish.

Chapter 4. Migratory mechanisms in Atlantic salmon.

4.1 Introduction

The aim of this review is to identify the mechanisms underlying the migration of Atlantic salmon in Scottish coastal waters. Ultimately, the review, when combined with empirical and modelling studies, will be used to (1) provide an account of coastal migratory routes based on likelihood, (2) identify crucial gaps in understanding in the particular context of marine renewables development, and (3) devise ways of prioritising and resolving requirements for additional data. The particular merits of attempting to identify and prioritise migratory mechanisms relate to the choice of geographical domain for hydrodynamic particle modelling, the introduction of particles intended to simulate migrating fish to the selected domain and, in particular, the choice of points of entry of particles across domain boundaries. The review is undertaken knowing that the research literature is currently insufficient to provide a definitive account of migratory mechanisms. The aim, therefore, is to provide a plausible provisional account based on a parsimonious synthesis of the available data.

Many species of salmon undertake long-range migrations before returning to their home rivers to spawn. Homing requires a capacity for direction-finding and the large distances traversed by returning adults and the disparate range of environments they cross (ocean, coast and river) suggest that different mechanisms are likely to be active at various stages. Salmon leaving Scottish rivers are most likely to encounter coastal or offshore renewables installations (arrays of wave energy converters, tidal turbines or wind turbines) near the start of their migration as smolts and, again, as adults on their return. Although oceanic migration takes place remote from any current possibility of interaction with marine renewables devices, consideration of direction finding mechanisms in the ocean is a necessary part of understanding migratory behaviour in coastal waters. Thus, the behaviours of smolts in coastal waters may anticipate oceanic behaviours, thereby affecting the routes by which fish leave the coast, and the oceanic behaviours of returning adults will determine the locations at which they enter coastal waters and, therefore, their transit routes through them.

Since the published literature on direction-finding in Atlantic salmon and other salmonids is not sufficient to support the review's objectives, consideration of potential mechanisms has been extended to non-salmonid species. In particular, it has been extended to other species that are able to navigate in fluid environments remote from any terrestrial frame of reference. Fluidity is a notable characteristic of the aquatic environment in the context of migration since, relative to the terrestrial frame of reference, the net movement of aquatic migrants is the result of not only their own active motion, but also any movement of their surrounding medium. In addition, the apparent lack of permanent features in the open ocean makes migrants particularly susceptible to the effects of advection and drift unless they have a well-developed capacity for direction-finding and position-fixing using the few cues that appear to be available to them. The aim of the wider review is to identify mechanisms from other species to account for gaps in understanding of the migration of salmon.

4.2. Migration

Migration has been considered under three domains – river, coast and ocean – since they differ so markedly in the range of potential directional cues that they appear to offer. It seems possible, or even likely, that migrating salmon use different cues, or mixtures of cues, in each domain. Within domains, mechanisms and routes have been considered separately for smolts and adults since it seems likely that some of the mechanisms used by smolts will differ from those used by homing adults. Most salmon originating in Scottish rivers make the journey only once and therefore any scope for using learned behaviours is restricted to returning adults using information acquired during the outward smolt migration. Even on those parts of the route shared by smolts and adults, mechanisms are likely to differ between outgoing migrants, with no prior knowledge or goals, and returning migrants searching for cues from their home river.

The simplest possible hypothesis is that migration is based on passive transport mechanisms associated with consistent natural features such as coastal currents or ocean gyres (Shelton et al. 1997; Dadswell et al. 2010; Mork et al. 2012). It would be surprising if these features were not exploited in some way since they are prominent in the environments in which migratory routes and behaviours have evolved. However, passive mechanisms alone cannot

account for salmon migration since the fish leave and return to a geographically diverse range of locations via a broad range of hydrodynamic conditions and coastal environments. For example, even in a Scottish context, the logistics associated with leaving and returning to the River Clyde (west coast) differ markedly from those associated with the contiguous catchment of the River Forth (east coast). In addition, for at least some part of the opposed outward and inward journeys, smolts and adults must use the same route and passive displacement cannot be invoked for both cases. On a broader scale, the general ocean circulation of the North Atlantic is not adequate to carry salmon consistently to their feeding grounds (or back to their countries of origin) within the timescales in which their migration occurs (Section 2.4.1.3). Directed swimming activity is, therefore, certain to be involved in both the outward and return migrations.

Nevertheless, advection is inevitable in the presence of marine currents. Swimming capacity scales with body-size and because they are relatively small, smolts will be particularly susceptible to drift. The maximum sustainable swimming speed of smolts (approximately 0.15 $m.s^{-1}$; see Section 4.7) is much less than the velocities of marine currents in some tidally-dominated regimes. It is possible that advection is assimilated into migratory pathways (Booker et al. 2008) or that it is wholly or partially compensated by contemporary directed activity, or by periodic compensatory activity as for marine turtles (Narazaki et al. 2009). Again, however, smolts in particular are small and their capacity for compensatory movement is low. Nevertheless, modelling studies indicate that even modest directional activity can substantially modify trajectories of moving animals, even where the principal influence is advection (Scott et al. 2012).

4.3. Homing

After a variable and prolonged period of outwards migration comprising directed swimming, random activity and drift, individuals originating from a single location are likely to end up widely distributed. Despite this likely spatial spread, the mechanisms used in the return migration have the effect of resolving this disorder since most fish ultimately return to their natal rivers. Even at a sub-catchment scale, many fish demonstrate the capacity to return to the minor streams that they inhabited before smolting (Youngson et al. 1994; Quinn et al. 2006). On the other hand, tagging studies show that some fish do stray to non-natal rivers.

For example, some fish tagged as smolts in the River Dee are captured as adults in fisheries within the nearby River North Esk (see Chapter 5). However, strayed fish like these are removed by fisheries on capture and therefore cannot correct any temporary homing errors. Indeed, studies of the movements of radio-tagged fish in the River Spey suggest that such straying is temporary for some fish and that the errors they make are rectified. Thus, around 20% of 69 adults captured and radio-tagged on entry to the river subsequently left it, often after extensive and prolonged journeys upstream, and one of these was later captured in the River Findhorn nearby (Laughton 1991). No more formal estimates of straying rate are readily available for salmon in Scottish rivers but based on tag returns in the catches of local fisheries, values for the River Imsa in Norway are reported to be ca. 6% (Jonsson et al. 2003). Even this low value is probably an over-estimate since, as before, the fish that had strayed were removed by fisheries several months in advance of spawning and potentially, therefore, before their migration had been completed. Overall, therefore, the great majority of adult fish can be considered to home to their natal areas before the return migration is fully complete.

4.4 Variation in migratory behaviour

The basic behavioural mechanisms that permit and sustain migration in all salmonid species are innate, although the set of behaviours (or the balance of their deployment) must differ among species. For example, Atlantic salmon and sea trout commonly co-occur in Scottish rivers but their smolt migrations differ markedly. The migration of sea trout is often only of local, coastal extent and they disperse over a wider range of directions which sees exceptional individuals recaptured in the southern North Sea (Nall 1930). In contrast, salmon are long-distance migrants that migrate towards northern locations in the ocean.

A consideration of the general diversity of salmon, particularly in the Scottish context, will prove of value in an initial screening of the various categories of mechanism that must be considered in order to account for the patterns of migration that are observed. Thus, for example, the coastal stage of migration must inevitably vary among populations originating from rivers distributed throughout the species' range. Even across the more limited spatial range of Scottish rivers, disparate entry points to the sea must require that different migratory mechanisms are used to achieve common destinations in the ocean or,

alternatively, that the achieved ocean pathways themselves must differ. At an even finer level, studies of chinook salmon demonstrate marked differences in the coastal distribution of smolts originating from different contributing populations within a single river catchment (Burke et al. 2013).

Considering temporal variation in the same way, sub-catchment structuring of populations (Verspoor et al., 2005) is associated with differences in sea-age (the number of winters elapsing between smolting and adult return). Thus, after entering the sea in May, fish allocate either ca. 14 – 18 months (grilse or 1 sea-winter fish) or ca. 21 -29 months (2-sea-winter fish) to their marine migration; some fish remain at sea for even longer but these are now uncommon. Within sea-age groups, the ranges in times spent at sea are generated by variations in run-timing (the date at which the home river is attained). Run-timing within sea-age groups is strongly heritable and therefore largely pre-determined (Hansen and Jonsson. 1991; Stewart et al., 2002). Thus, in Scotland, the earliest-running 1SW fish return to rivers around May and June and the latest-running 1SW to do so around November. Among 2SW fish, the earliest-running fish reach rivers around January while the latest-running do so around November. Given these large variations in return timing, marine and coastal migratory schedules must necessarily differ among the different sea-age and run-timing groups. If migratory distance achieved varies with time elapsed, the extents of their excursions from the home river probably also differ. All these variations must be matched either by variations in the underlying migratory mechanisms or, more probably, by variable modulation of shared mechanisms. It is important to note that because adults show such wide variations in the time they spend at sea, no aspect of the return journey is likely to be a response to seasonal variation in any of the oceanic features (e.g. sea surface temperature or its correlates) that might otherwise be proposed as cues.

4.5. Orientation and navigation

Judging by what is known for other species which have been more fully researched (Bingman & Cheng 2005; Wiltschko & Wiltschko 2012), it is likely that migration is based on a composite of mechanisms. Proximal cues are lacking for both smolts and adults as they transit the open ocean, and since salmon are considered to be epipelagic (they mostly exploit shallow surface waters) they have no direct access to a terrestrial frame of

reference. Orientation of swimming activity must, therefore, be based on compass mechanisms using only those cues that are available in the marine environment. For example, for fish in shallow waters the position of the sun in the sky is a direct indicator of south in the northern oceans. Additionally, salmon are capable of detecting polarized light (Flamarique & Hawryshyn, 1997) and celestial patterns of polarization, averaged for dawn and dusk, potentially indicate the north-south axis (Willis et al. 2009). However, for salmon in the northern oceans in winter, any light-based orientation mechanisms will be impeded or precluded, especially at higher latitudes.

The geomagnetic field may provide a more consistent directional indicator for salmon, as it appears to do for other migratory species (Berthold & Helbig 1992). Indeed, the recent demonstration that cells from the olfactory epithelium of a salmonid species rotate in response to changing field direction because they contain single-domain biogenic magnetite, provides the first direct evidence of a potential magnetic transducer mechanism (Eder et al. 2012). An alternative, or complementary, visual mechanism for magnetoreception and direction-finding is proposed based on the sensitivity of retinal cryptochrome in some bird species to variations in magnetic field (Ritz et al. 2009; Stapput et al. 2010).

Many migratory species show an innate ability to align with the Earth's geomagnetic field. These biases determine direction of migration and are therefore likely to be adaptive (Berthold & Helbig 1992). Experiments on migrant birds show that the directional preference for flight reverses seasonally, in line with expectations based on the observed movements of free-living birds (Wiltschko & Wiltschko 1991). In natural situations this bi-polar mechanism may become partially obscured by factors based, for example, on learned behaviours (Able and Able, 1996). Salmonids are sensitive to the geomagnetic field (Quinn 1980; Quinn et al. 1981; Quinn & Brannon 1982; Taylor 1986; Chew & Brown 1989; Walker et al. 1997). It is therefore plausible that they also show geomagnetic directional biases that are innate and that these could form a basic template for migration. In some cases, biases differ among populations of avian species in a manner that can be interpreted as adaptive (Berthold & Querner 1981). Salmon show genetic population structure that is spatially organised and populations differ in many respects that can be construed to reflect genetic

adaptation (Garcia de Leaniz et al. 2007). It is also possible, therefore, that a directional bias in swimming during migration is a characteristic that varies among salmon populations. Such a mechanism might result in smolts originating from different rivers around the Atlantic converging upon common feeding areas. Equally, it might allow divergent routes among adult fish returning to different rivers from a shared starting location in the ocean.

A directional sense alone is not sufficient to locate a target position. Thus, solar cues are insufficient for position-fixing and navigation in the presumed absence of a precise, innate calendar and clock. Likewise, directional geomagnetic cues are insufficient for navigation in the absence of a bi-coordinate map. It has been suggested that an ability to detect intensity or angle of inclination of the magnetic field (Putman et al. 2011) provides the capacity to fix an approximate latitudinal position for some marine migrant species, including salmonids (Hellinger & Hoffmann 2009; Bracis & Anderson 2012; Putman et al. 2013). A possible mechanism for longitudinal position-fixing remains particularly problematic, although it has been suggested that geomagnetic field anomalies may indirectly support this capacity (Walker et al. 1997; Walker & Dennis 2005; Lohmann & Lohmann 2006) for species including salmonids (Alerstam 2006; Lohmann et al. 2008). In the case of sea turtles, for example, experimental studies demonstrate that naïve individuals show different swimming responses in imposed magnetic fields that are designed to simulate conditions at the same latitude but at different longitudes on opposing sides of the natural ocean range. The directional swimming responses are consistent with the behavioural characteristics of free-living turtles in the same areas (Putman et al. 2011). An innate, bi-coordinate map of the geomagnetic range is therefore proposed coupled with a capacity to modulate directional behaviour in the context of a bi-coordinate positional sense (Lohmann et al. 2011). Boström et al. (2012) consider the relative alignments of field intensity and inclination isolines at the global scale to provide an assessment of the likely scope for bi-coordinate geomagnetic navigation across the Earth's surface.

4.6 Migration by salmonids of Scottish origin

Many tagging studies have been carried out on Atlantic salmon in Scotland and these disclose patterns of movement (but not the intervening pathways) when tagged fish are recaptured in fisheries (Chapter 5). Tagging studies are of two main types. In the first, smolts

of known origin are tagged in home rivers near the start of their migration. Because of their small size, juveniles are not susceptible to fisheries but tagged fish of known origin are recaptured as adults in distant oceanic fisheries and in coastal or river fisheries on their return to homewaters. In the second class of study, adults of unknown origin are tagged in distant or homewater fisheries and recaptured by other fisheries en route to, or in, their presumed rivers of origin. In addition, some more recent studies have used river- or region-specific genetic markers to infer the origin of fish captured in commercial or experimental fisheries, notably the SALSEA-MERGE (2012) programme.

Salmon are present in most rivers of the Scottish mainland and the Western Isles; they are absent from the Orkney and Shetland Islands because these lack substantial rivers. At sea, commercial fisheries for salmon are generally pursued where fish and fishermen are in relatively close proximity. Because of their remoteness, large areas of the North Atlantic Ocean have never been tested for the presence of salmon but the proven marine range of salmon tagged in Scotland is shown schematically in Figure 4.1.

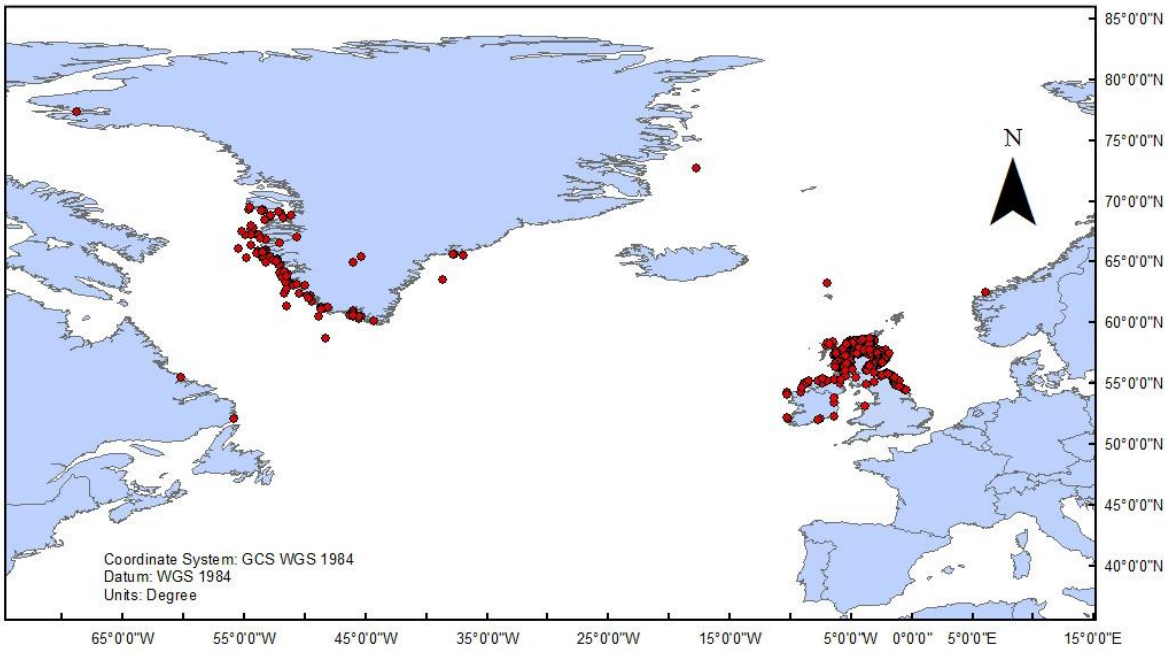


Figure 4.1 Recorded distributions in the North Atlantic of Atlantic salmon originating from Scottish rivers. Locations were obtained from tagging studies of smolts and adults carried out in Scottish waters over the last 120 years. Because multiple fish can be caught at a single location, individual points do not necessarily correspond with individual recaptures. Hence, the figure provides an indication of the distribution of Scottish salmon and cannot be used for more quantitative interpretation.

Soon after leaving Scottish rivers, juveniles are captured in research fisheries around the continental shelf edge to the northwest of Scotland and in the Norwegian Sea (SALSEA-MERGE 2012). Adults from Scottish rivers are known to be present at West and East Greenland (Reddin et al. 2012), in Faroese waters (Jacobsen et al. 2012), in Irish coastal fisheries (Went 1973; Went 1976), and in inshore waters on the UK east coast as far south as Yorkshire (Potter & Swain 1982). Interestingly, distributions shown in Figure 4.1 apparently contradict statements about capture of Scottish fish in the Faroese fishery. This absence of recaptures is due to the temporal mis-match between the main tagging experiments (1901-38 and 1968-70s) and the duration of the main Faroese fishery (1979-90; ICES 2012). Scottish salmon are very infrequent in fisheries on the eastern (Norway and Sweden) and western Atlantic coasts (Maritime Canada). In home waters, the apparent historical absence of commercial fisheries in Orkney and Shetland, despite the local cultural affinity with fishing and the past prevalence of salmon fisheries on the nearby coasts of Caithness and Sutherland, is surprising and possibly noteworthy (Malcolm et al. 2010).

4.7 Coastal behaviours of smolts

Prior to marine migration, juvenile salmon exploit freshwater habitat distributed throughout most Scottish rivers. Juveniles feed and grow in the same general vicinity for a year or more before they undergo the physiological, behavioural and conformational changes associated with smolting (McCormick et al. 1998). Age at smolting is growth- and size-dependent and, in Scottish conditions, smolts are typically two or three years of age and 120 -150 mm in body length when they leave their rivers. By this stage, their appearance and behaviour has changed from that typical of cryptic, bottom dwelling fish to the silvered condition more typical of shoaling, pelagic species. Smolts move downriver in spring and, in Scotland, enter the sea around May.

The behaviour of Atlantic salmon during the outward migration through the coastal domain is only sparsely documented. The research literature for Pacific salmon species is similarly sparse and offers no particular insights in the present context (see Quinn 2005 for a synthesis). For Atlantic salmon, a recent assessment of the limited evidence is provided by Thorstad et al. (2012). Studies have been biased towards monitoring activity in sheltered waters suited to the use of acoustic tags and receiver arrays. Such habitats differ markedly

from the coastal and oceanic conditions encountered by smolts leaving the major rivers of eastern and northern Scotland. In addition, the studies are often of cultured smolts which may perform differently from wild smolts because of the effects of the rearing environment and because their early marine migration is not preceded by a riverine phase. Moreover, groups of migrants may demonstrate more coherent patterns of behaviour (Simons 2004; Herbert-Read et al. 2013) than single fish that have been tagged and released individually. Finally, the acoustic tags used to observe patterns of movement have the potential to affect the fishes performance (Perry et al. 2013).

Nevertheless, a summary of the data suggests that, from the outset of the marine migration, smolts mainly swim within the surface layers, moving offshore at speeds consistent with a likely maximum sustainable value of around 1 body-length per second ($bl.s^{-1}$). Estimates of rates of movement are relative to the terrestrial frame of reference and the wide limits on the observed range probably result partly from the effects of advection by currents. Even in sheltered fjordic locations, however, upper estimates suggest ground speeds in the range of 0.5 – 1.5 $bl.s^{-1}$ and, therefore, achievable gross daily movement of approximately 10-30 km per day.

There is no direct evidence to suggest how this capacity for movement is translated into a directional track within Scottish waters. In an evolutionary context, it might be expected that consistent hydrodynamic features of coastal waters will have been incorporated in these routes and that parallel behavioural adaptations will facilitate the exploitation of directionally advantageous currents and the avoidance of adverse ones when they can be detected. A weak residual circulation (the Scottish Coastal Current) directed clockwise around the landmass is a consistent feature of the Scottish coastal zone (Section 2.4.1.3). This current will tend to carry smolts originating in western rivers to the north, towards the marine feeding grounds, and those originating in eastern rivers southwards, away from them. These displacements are, however, net effects because, at times, reversing tidal effects or wind forcing will mask or exceed the effects of circulation patterns on water displacement and advection. In such conditions, adverse effects on migratory progress might be avoided by using selective transport mechanisms, such as seeking refuge from adverse currents (Harden Jones et al. 1979). However, there is no evidence for this type of

behaviour in Atlantic salmon and, in any case, fish swimming in the surface layers of open waters of even moderate depth have no obvious means of assessing changes in their ground speed and therefore no obvious basis for a behavioural response.

For many years nothing was known of the post-smolt period in any part of the North Atlantic beyond sporadic reports of fish taken as by-catch in commercial fisheries. More recently, experimental fisheries carried out in the summer months using surface trawls have located aggregations of smolts northwest of Scotland and Ireland and in the southern and central Norwegian Sea (Shelton et al. 1997; Holst et al. 2000; Holm 2000; Holm et al. 2003). The recently completed SALSEA-MERGE (2012) project was undertaken to extend and formalise earlier work and, in particular, to use genetic assignment methods to allocate smolts to their regions of origin. As a general summary of the approach, genetic variation was examined in a baseline set of samples obtained from juvenile salmon in a large number of rivers across the European range. These data were used to allocate individual rivers to quasi-regional groupings of shared genetic character. Based on their genetic characteristics individual smolts captured in the ocean were then assigned to these regional groupings. Using the chosen genetic methodologies, 18 regional groupings were identified covering the European distribution of salmon rivers from Kola and Iceland groupings in the north and west, respectively, to a single South France and Spain grouping at the southern extreme of the species' range. Two genetic groupings contained Scottish fish: (1) South and East Scotland; and (2) North Scotland and West Ireland. It is important to note that these groupings were based on statistical assessment of genetic similarity and that, as the terminology suggests, they did not resolve as discrete geographical units. Genetic analysis of smolts captured in the ocean shows that both of the groupings that include fish assigned to Scottish rivers are well represented throughout the fishery area. In particular, fish classed as originating in the South and East Scotland river grouping are already represented to the west of the Hebrides in the period May – July. It may be that fish originating from the more westerly of the rivers in this grouping move rapidly north and westwards to reach the area and that all the smolts assigned to the grouping originate from this western component. However, the South and East Scotland grouping constitutes a large proportion of all the fish captured in the area. Given the large productive capacity of the eastern rivers component of the grouping relative to the western component, it may be that smolts originating in the

eastern rivers also reach the area in question by moving quickly north and westwards against the Scottish Coastal Current.

This latter point cannot be resolved using the information that is currently available. However, the point is crucial in considering whether the outward route for smolts from the large eastern rivers is biased westwards through the Moray and Pentland Firths (both of which are areas of renewables development) or northwards through the central or eastern North Sea. Those involved in the SALSEA-MERGE project advise that it is now likely that smolts could be assigned to Scottish rivers at the required, finer level using genetic markers that were not available at the time of the original project (see Verspoor et al. 2012). On this basis, re-analysis of the existing samples using the new set of genetic markers would support strong inferences on the likely coastal routes of smolts originating in the large rivers of the Scottish east coast.

4.8 Behaviours in the ocean

Access by smolts to the southern Norwegian Sea raises a range of possibilities for further progress to all areas of the northern Atlantic, perhaps facilitated by consistent patterns of circulation towards the north and the northwest (Fig. 2.1). Present knowledge of the distribution of fish of proven Scottish origin in the distant ocean is based only on tagging data derived from the fisheries that have operated at various times around Greenland and the Faroe Islands. Tagging studies show that salmon are capable of moving between the Greenland and Faroe fishery areas and that some fish originating in rivers along each of the opposing Atlantic coasts reach the more distant of the two fisheries (Hansen & Jacobsen 2003). However, the data also show that fish from the eastern and western Atlantic rivers are not uniformly distributed across the area known to be used by salmon, but instead are biased towards areas nearer their source (Jacobsen et al. 2012; Reddin et al. 2012). Thus, for example, fish from the Russian and northern Norwegian rivers dominate in the northern Norwegian Sea but are under-represented in the western Atlantic and fish of North American origin dominate at Greenland but are under-represented further east. The distribution of Scottish salmon is probably biased in a similar way, since their contribution to the Faroese and Greenland fisheries is greater at lower latitudes (Hansen & Jacobsen 2003).

Salmon of proven Scottish origin contribute substantially to both the Greenland and Faroese fisheries suggesting a similarly broad east-west pattern of distribution throughout the northern North Atlantic. The routes and timings by which salmon enter the fishery areas and their distribution outside these areas are not known. Moreover, most of the available tagging data refer to Scottish fish that subsequently matured at the 2 sea-winter rather than the 1 sea-winter stage and the range and direction of travel for the 1 sea-winter group are therefore largely unknown. Because of these knowledge gaps, it is not possible to specify inward routes from the ocean towards the Scottish coastal domain. More generally, however, since the duration of the feeding phase at sea varies substantially (typically over a 14 – 29 month range), it seems likely that the extent of the marine ranges of different sea-age and run-timing groups differs. This position is supported by stable isotope studies demonstrating differences in the marine diet among groups of fish returning to UK rivers (MacKenzie et al. 2012) and differences in marine growth performance (Bacon et al. 2009). The marine distributions of fish with different run-timings and of different sea-ages may well vary in the same way judged by patterns of tag recovery (Satterthwaite et al. 2013), differences in stable isotope ratios (Johnson & Schindler 2012) and variations in temporal patterns of abundance (Youngson et al. 2002). Accordingly, the points at which adult fish begin their homeward spawning migration may well vary among both sea-age and run-timing groups and individuals must therefore be considered likely to approach Scottish coastal waters on a wide range of headings with different origins in the northern and western Atlantic Ocean.

For inward migrant Pacific salmon, tagging studies show that the net distance moved between release and recapture positions is close to predictions for maximum sustainable swimming speed, suggesting near straight-line trajectories (Quinn et al. 1989; Ogura & Ishida 1995; Tanaka et al. 2005; Crossin et al. 2007). Indeed, direct observations of tagged fish shows that they maintain constant directional courses for periods of days, maintaining direction both by day and night (Ogura & Ishida 1995; Crossin et al. 2007). But even if individuals maintain a consistent heading, patterns of return of Atlantic salmon from the ocean to the Norwegian coast suggest that inward accuracy relative to the home river destination is low. Thus, returning adults were captured in coastal patterns biased far to the north of their target river (Hansen et al. 1993). However, the same patterns might be

generated if adults returned accurately to a transitional position on the coast, for example, the point from which they left the coastal zone as smolts after a period of inshore movement, northwards with the Norwegian Coastal Current.

In Hansen et al.'s (1993) study, the coastal patterns of recapture for four rivers distributed along the Norwegian coast were shown to be qualitatively different; fish originating in southern rivers showed a southern bias in spatial distribution in the coastal fisheries relative to fish originating in northern rivers (Fig. 4.2). If the patterns of recapture reflect the coastal track of the river groups, their spatial separation could arise from regional or river-specific differences in the inward heading from the ocean to the coast. Indeed, there is some evidence that the inward heading from the ocean is innate, or partly so, since farmed salmon of Norwegian origin released in Scotland were recaptured only in western Scandinavian fisheries, a pattern of distribution unknown for wild fish of Scottish origin (Hansen & Youngson 2010). Indeed, innate headings of high specificity are reported for other migrant species and for populations within species (e.g. Berthold et al. 1992).

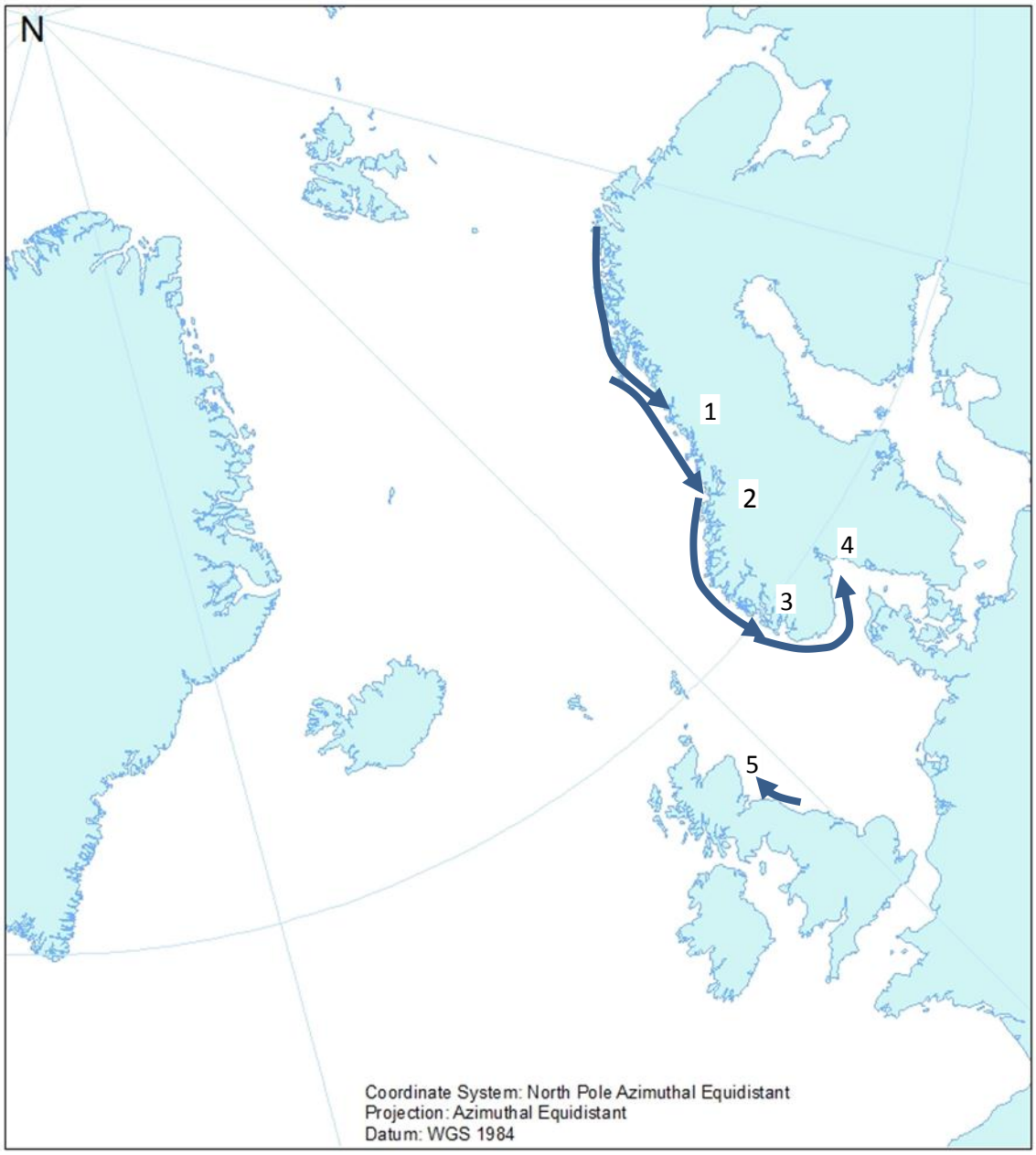


Figure 4.2. Diagram showing coastal distributions of tagged Atlantic salmon returning to the Rivers Vefsna (1), Nidelva (2), Imsa (3) and Sandvik (4) in Norway (Hansen et al. 1993) and to the River North Esk (5) in Scotland (Potter and Swain 1982). Salmon from each river, which were tagged as departing smolts, were mostly recaptured somewhere along the coastline covered by the length of the arrow, where the arrowhead indicates the home river. The arrows along the Norwegian coast illustrate that fish from different rivers each return to an appropriate region of the coast, but with limited accuracy, biased to the north of their home river. This northward bias of recaptures has been interpreted as fish returning to the north of their home river and then swimming south against the Norwegian coastal current to return to their home river (Hansen et al. 1993). The arrow on the Scottish coast illustrates the northward sweep of fish returning to the River North Esk (5) as described by Potter and Swain (1982). Routes of return migrations are straightforward for the Norwegian fish, where a direct approach to the coastline is possible from feeding grounds around the Faroe Islands or Greenland. It is more difficult to explain how fish leaving from presumably similar areas travel to the east coast of Scotland to end their migration moving North towards their home river.

In a Norwegian context, therefore, the simplest schema requires that salmon returning from a westerly or north-westerly position in the ocean use directional cues to adopt an inwards heading to reach an area of the coastal zone from which they can re-orientate southwards against the Norwegian Coastal Current towards their home river. However, the distribution of Norwegian salmon rivers relative to the ocean feeding grounds differs markedly from the distribution in Scotland. Most of the Norwegian rivers are open to a direct approach from the ocean while the most productive Scottish salmon rivers are shielded from it by the UK landmass.

For most Norwegian salmon, a single approach heading, subject to minor coastal re-alignment, would be sufficient to provide access to the vicinity of most home rivers. In contrast, a more complex, two-stage strategy would be necessary for any fish returning directly to the Scottish east coast from a presumed starting position to the northwest. An easterly or south-easterly course would be required to pass to the east of Shetland, for example, but an opposing south-westerly course would then be required to reach the eastern coast of mainland Scotland. Furthermore, this change in course would have to be executed in the northern North Sea, remote from any coastal cues, and would have to be perfectly executed since tagged fish of Scottish origin are unknown from the coastal fisheries of southern Norway.

The alternative scenario envisages a direct parallel with the Norwegian situation, in which fish of Scottish origin set courses to intercept the regional landmass, making requisite adjustments to route in the coastal domain. Thus, for example, fish returning to rivers in western Scotland might offer an exact parallel with the patterns described by Hansen et al. (1993) by making landfall to the north, re-aligning and proceeding southwards. In another almost exact parallel, Scottish fish returning to the rivers of the east coast might approach the entrance to the Pentland Firth, re-align using coastal cues and pass almost directly to the coast beyond. However, from a plausible starting point at the southern tip of Greenland, the latter case would require a high level of directional precision (ca. +/- 1 ^{o}). From the same starting point, less precision would be required to intercept the western Scottish coastal zone between, for example, Westray and the Mull of Kintyre (ca. +/- 6^{o}). In this latter case, however, the direct analogy with the Norwegian situation would break down since more

complex mechanisms would be required to account for the reversal of heading required to target the eastern coastal domain using western coastal cues.

4.9. Coastal behaviours of adults

As they near the coast, returning fish are afforded the opportunity to replace or tune their course according to a new range of sensory cues. Relative to the ocean, the coastal domain is geographically complex and therefore more complex orientation mechanisms are probably required. Salmon must be aware of the coastal profile or the proximity of the shoreline since they avoid stranding and the same cues could be used to support coastal orientation. Again, this aspect of salmon behaviour has not been investigated. However, the behaviour of reef fishes has been extensively examined and some of the features of their biology are somewhat analogous to those of salmon. In particular, juveniles of many reef species must relocate to reef habitat after dispersal as eggs and early-stage juveniles and they do so by directed activity towards favourable habitat using a range of cues (Montgomery et al. 2006). Water chemistry, olfaction, sound and vibration have all been implicated in these directed movements (Kingsford et al. 2002; Huijbers et al. 2012). Although there are no exact parallels, the reactions of reef fish to local directional cues may cast light on the range of responses that may be available to salmon migrating in the coastal zone.

Variables such as temperature and salinity do not offer a reliable basis for orientation over long coastal migrations. Given the typically complex hydrodynamics of coastal waters, they are likely to vary inconsistently and unpredictably. In shallow waters, vision may offer more robust cues. Indeed, the effectiveness of the commercial “jumper” nets of the Scottish east coast fisheries (which fish only over the inter-tidal zone of sandy beaches), shows that near-shore areas, where visual cues are possible, are consistently used by some migrating salmon. However, visual cues will be compromised by low light intensity at night or by the turbidity that is characteristic of some coastal environments. Sound may offer more consistent cues for orientation by coastal migrants since salmon are capable of locating the directional position of a sound source (Popper & Schilt 2008). If shore noise can be distinguished from other sources of ambient noise, a response may be possible. Thus, if salmon can detect directional variation in sound intensity or if they can locate spectral

qualities that distinguish the near-shore area generated, for example, by the dissipation of wave energy, they may be able to construct an auditory representation of the coastal profile in their near vicinity. Such a mechanism could be used both for avoidance and orientation during coastal passage.

Salmon sense only low frequency sound(< approximately 380Hz) relative to other fish species, since they lack a functional connection between the swim-bladder and the auditory apparatus (Hawkins & Johnstone 1978). In particular, they sense infrasound (i.e. < approximately 20 -50 Hz) (Knudsen et al. 1992; Enger et al. 1993; Sand et al. 2001) which is particularly likely to propagate over long distances (Popper & Schilt 2008; Bardyshev 2008). Abiotic ambient noise in the marine environment is mostly attributable to the dissipation of wave energy which generates sound across the range of frequencies detected by salmon, down to infrasound values (Radford et al. 2008; Cho & Choi 2009). In particular, random turbulent-pressure fluctuations, which are likely to be a particular feature of the shoreline, generate low frequency sound (Knudsen et al. 1948; Wenz 1962). In a related context, interference of incoming and reflected waves at the coastal interface also dissipates energy to generate the characteristic double-frequency microseismic events that, again, are a particular feature of the coastal environment (Kedar & Webb 2005; Aster et al. 2008).

Sand and Karlsen (2000) have hypothesised a role for infrasound in the long-distance ocean migration of Atlantic cod. In similar vein, Slabbekoorn and Bouton (2008) and van Opzeeland and Slabbekoorn (2012) develop a generalised “soundscape” concept. However, the shallow waters of the near-shore zone are likely to be a sink as well as a source of sound since physical features modify propagation and sediments tend to absorb sound energy, particularly in the low-frequency part of the range. Wahlberg and Westerberg (2005) describe an approach based on theory for estimating the range of detection of underwater sound over the range of wave-lengths generated in a very specific context (by a single wind turbine operating in coastal waters). They found the detection range for salmon (at 100 Hz) to be much less than for the other species considered due to physiological differences and only about 500 m for a wind turbine operating at moderate wind speed. They emphasised the difficulties posed for estimating range by the weakness of supporting knowledge, a point repeated in a similar context by Thomsen et al. (2008). Even so, although a similarly

short range of detection for coastal noise would not support long-distance orientation, it would support avoidance of stranding and coastal alignment in the near-shore area. Even in the absence of a specific alignment mechanism, avoidance alone would result in *de facto* coastal alignment for salmon attempting to maintain a preferred heading but prevented from doing so by the proximity of the shoreline**.**

In some circumstances, salmon reaching coastal waters need only make a small adjustment to their existing heading using whatever coastal cues exist in order to continue the approach to their home river. However, in the plausible case of a fish reaching western coastal waters, but judged from tagging data to be attempting to return to an east coast home river, progress will be prevented by the north-south alignment of the Scottish coast. Even if the present and home river positions are somehow known, this presents an obvious dilemma as to whether to correct northwards or southwards of the landfall position in search of access to the east coast and it also raises the question of what mechanisms might support an appropriate change of course.

There appear to be two possible mechanisms:

1. By direct analogy with patterns of migration previously inferred for coastal migration in Norway, minor directional accommodation of incoming fish and continued southwards travel along the west coast could deliver fish to their destination on the Scottish east coast via the English Channel. This possibility is not inherently unlikely since such a pattern would be analogous to the approach to the River Sandvik in Oslofjord (Fig. 4.2) as documented by Hansen et al. (1993), differing only in scale. It would also accommodate the observed presence of large numbers of fish belonging to the rivers of the Scottish east coast on the Yorkshire and Northumberland coasts and the northwards travel observed when such fish are tagged (Potter & Swain 1982). However, the absence of any tagging evidence for an extreme, southern distribution of Scottish fish beyond occasional returns from Irish fisheries and the abundance of tagging evidence placing adult fish of eastern Scottish origin on the north coast (Malcolm et al. 2010) weigh in favour of a northerly course.
2. Northwards re-orientation could be supported if the latitudinal location of passage was known to the fish. This could be based on a less-constrained variant of the geomagnetic imprinting mechanism recently demonstrated for the home river location for Fraser River sockeye salmon (Putman et al. 2013). The variant now proposed invokes geomagnetic imprinting during the coastal passage of smolts rather than, or as well as, at their point of departure from the home river. The variant mechanism would account for Hansen et al.'s (1993) description of the

return of adult salmon from the ocean to Norwegian rivers via river-specific coastal areas that are remote from the home river but plausibly on the smolts' outward route to the ocean. If the latitudinal positions of these areas are imprinted, perhaps as the smolts' point of departure from the coastal zone, adults might target them as a way-point on the return route. In Scotland, the analogous scenario would extend to include imprinting to the latitudinal position of westwards passage to the ocean. In the particular context of the Pentland Firth, it follows that any adults originating from the east coast, using a latitudinal sense to seek eastwards passage through the Firth must have passed through, and imprinted on it, at the smolt stage. Large numbers of adults of east coast origin are likely to pass through the Pentland Firth (Malcolm et al. 2010) but an opposed outwards route for smolts is unproven. Re-analysis of the SALSEA-MERGE samples might resolve this important point, as discussed previously.

4.10 Behaviours near the home river

Successful coastal migration brings adults towards the home-river domain. At this stage consideration of behavioural mechanisms tends to be dominated by the home-stream odour hypothesis (Hasler & Wisby 1951; Scholz et al. 1976). This proposes that smolts learn the unique olfactory signature of their river of origin, retain these memories and, as adults, return to their original location by discriminating home-river odours among those issuing from other rivers. The hypothesis is based on experimental field evidence obtained by manipulating stream odour using synthetic organic compounds. Natural cues might be biotic or abiotic and the former might include odours attributable to conspecifics (Nordeng 1977). A functional mechanism for the retention of memories has been proposed based on the permanent modification of olfactory receptors (Nevitt et al. 1994; Dukes et al. 2006; Johnstone et al. 2012).

Subsequent field experimentation based on physical re-location of salmon of various sources and treatments has suggested a more complex, sequential imprinting model as originally proposed by Harden Jones (1968). This concept requires that adults follow (in reverse) a sequence of cues imprinted during their outward migration as smolts. Reared smolts raised in river water but liberated at sea, and which have not therefore undertaken the river and near-river migration, return as adults to the general vicinity of the rearing place but delay entering fresh water or fail to do so (Hansen et al. 1987; Jonsson et al. 1990; Hansen et al. 1993). This suggests that any odour memory forms only part of the sequential

imprinting process. These studies have not identified the set of sequential cues nor their spatial extent along the migratory route. Presumably, candidate cues must be permanent biological, structural or environmental features of the river, or near-river, environment and they must be sampled by outgoing smolts and by returning adults. Both groups of fish must therefore use functionally coincident routes over the series of imprinted locations. Smolts go to sea in May, but adults return to Scottish rivers in every month of year so the presence of the cues must be independent of season. Imprinted geomagnetic information (Putman et al. 2013) may form part of the set of sequential cues. The set probably also includes the olfactory cues central to the home-stream odour hypothesis. If so, river plumes represent a variable but sometimes extensive connection between the river and coastal domains and may be a crucial determinant of behaviour in the final stage of the return migration.

The general pattern of Scottish coastal circulation is driven in a clockwise direction by the Coriolis effect. The coastal currents are relatively weak and therefore susceptible to modification, including reversal, by other drivers such as tides and wind-forcing. On a local scale, general patterns of circulation will also be modified by the coastal profile and bathymetry but residual speeds are ca. 0.1 $m.s^{-1}$. Rivers discharge fresh water into this marine circulation. The pattern of dispersal of river water is governed by the movement of the coastal currents and by differences in salinity, and therefore density, between the water types. The spatial extent of the freshwater effect in the coastal domain is principally determined by river discharge and the energetic state of the receiving marine waters.

On a world scale, the behaviour of the plumes generated by very large rivers has been well-studied (e.g. Wiseman & Garvine 1995). As a general description, river discharge protrudes into the marine zone according to its mass and velocity, moves to the surface as a result of its lower density and spreads outwards to form a plume. The plume moves away from the river with the coastal current, tending to adhere to the coastline, and eventually dispersing along its leading edge due to mixing with sea water.

On a world scale, most Scottish rivers are comparatively small and their plumes may not propagate in line with this general description because of non-linear scaling effects in the underlying processes. However, direct observations have been made on some rivers in the relevant size class. For example, the Shannon in Ireland generates a visible surface plume

that is large, irregular and variable in form (Huang et al. 1993), affecting a surface area of up to 100 km^2 that extends northwards for approximately 70 – 100 km. As expected, the size of the plume varies with river discharge but it remains a prominent feature of the coastal waters even at low discharge values. For the Mooloolah River in Queensland, a river discharge event of approximately 20 $m^3.s^{-1}$ resulted in a visible plume extending approximately 1 km offshore and approximately 2.5 km along the coast (Gaston et al. 2006). The River Teign in Devon discharges tidally from a lagoon to generate a plume that was observed to extend at least 3 km off-shore (Pritchard & Huntley 2006). The visible dimensions of plumes are likely to underestimate the real extent of their influence given the diffuse nature of the boundary zone between fresh and sea water. The plumes of the larger Scottish rivers will therefore be kilometre-scale features of the coastal domain at all times; the plumes of the smaller rivers will tend to be less extensive at basal flows but prominent features at times of high discharge. Plumes will tend to move northwards on the west coast but southwards on the east coast in line with the prevailing coastal currents.

In order to move across the boundary between the coastal and river domains, homing salmon must deploy strategic behaviours to sample plumes (including those of the smallest rivers), distinguish the home river plume from others and move along the plume gradient towards its source. The latter behaviour corresponds to a special case among a set of search strategies described by Vickers (2000). Typically, the main strategy is to move towards an odour source using cross-current hunting to resolve spatial inconsistency in the signal gradient caused by the effects of turbulence. Notably, some of the migratory behaviour predicted on this basis is displayed by fish approaching the rivers of the Scottish east coast. Thus, many tagged salmon approach the rivers such as the Tay, North Esk and Dee by moving northwards against the coastal current (Potter & Swain 1982; Chapter 5) - contrary to the presumed southwards direction of their previous travel. Furthermore, the patterns of coastal capture of fish from these different rivers differ; fish from the more southern rivers have a more southerly distribution in the coastal fisheries. This suggests that the location of the reversal in heading from southwards to northwards is determined by some aspect of the location of the home river itself.

Reversal of travel might therefore be a direct response to odour, following interception of the eastern edge of the home river plume, down-current and, therefore, generally to the south of its source. However, the presence of large numbers of Scottish east coast fish off the Northumbrian and Yorkshire coasts, and probably distant from the effects of their home-river plume, weighs against an odour-led reversal mechanism. Moreover, the Tay, North Esk and Dee are relatively large rivers and a general mechanism must also support homing to small rivers with less prominent plumes. It has already proved necessary to invoke latitudinal imprinting by smolts to their points of departure from the coastal domain to explain aspects of migratory behaviour on their return there as adults. It may be that directional reversal and coastal searching for odour signals are supported by the same type of mechanism.

Putman et al. (2013) use a long-term data-set to demonstrate a behavioural response to secular variation in the geomagnetic field by sockeye salmon approaching the Fraser River in Canada. Over a period of decades, these fish have shown a variable bias in the use of the alternative southern or northern routes around Vancouver Island which are separated by around 400km. Fish tend to enter the route that, at the time, is more similar to the geomagnetic condition prevailing at the home river itself. The authors propose that route choice is dependent on a mechanism by which fish follow an isoline for an imprinted field-intensity value through the ocean towards their home river. It is not plausible to propose a similar isoline-following mechanism in the context of the eastern Scottish rivers because the final approach of tagged fish towards rivers is essentially south to north and therefore at ca. 90^{o} to the isolines for field values. However, it is not necessary to propose that the imprinted latitude of the home-river provides a precise cue for its location. Instead, the mechanism need only act as an eventual check on southwards coastal movement beyond the imprinted latitudinal value for the home river, particularly if the check is coupled with a northwards return. Equally, in a similar but opposed context, a symmetrical check on northwards movement beyond an imprinted latitudinal cue and a southwards return might constrain migration in a similar way. In the context of modelling, the distance observed to be associated with the southwards limit to the overshoot of fish returning to the east coast rivers (approximately 150 km in the case of the North Esk) may provide an operational measure of the precision of the proposed latitudinal sense.

Finally, in an even more general context, the same pair of check mechanisms might constrain the inwards course of adult fish returning from the ocean by acting to limit southwards (or northwards) deviation from the speculated imprinted latitude for the point of coastal departure. This proposal has the merit of invoking a single set of mechanisms to support both postulated instances of latitudinal imprinting and it accommodates the discrete but dispersed pattern of western coastal landfall made by tagged fish of Scottish origin (Fig. 4.1).

4.11 Conceptual model of Scottish coastal migrations

Many mechanisms for migration in salmon have been proposed in the research literature. Some are supported by reasonable experimental or field evidence while others are highly speculative. As for avian migrants, many mechanisms may be in play at various times or conditions (Thorup et al. 2010). Nevertheless, one of the aims of this review has been to identify a minimal set of mechanisms to assist in realistic parameterisation of particle-tracking models. A tentative rationalisation of possible mechanisms follows based on the evidence previously cited. However, since there is little direct evidence, a subsidiary aim of this approach is to present a "straw man" to be refined or replaced according to an alternative interpretation of the existing evidence or based on future studies.

The proposed scenario requires the following, minimal set of assumptions on migratory mechanisms, each of which can be plausibly justified based on the evidence reviewed in this document:

- Migrating smolts have an innate directional preference that is approximately reversed in returning adults.
- Salmon have an approximate sense of latitude based on a geomagnetic sense.
- Smolts imprint to the latitudinal position of their home river and also to their point of departure from the coast.
- Salmon have a sense of the coastal profile and align to it in the coastal domain.
- Smolts imprint to home river odours.

It is proposed that for salmon originating in Scottish rivers:

1. Smolts direct their migratory activity towards an innate heading. A preferred heading centred around geographical north-west is proposed in order to account for

the presence of Scottish smolts in western Hebridean waters and the southern Norwegian Sea

2. The possibility of direct headings being impeded by the coastal profile follows from the assumption of an innate heading and requires an escape mechanism. Temporary, partial reversal of heading is proposed, noting that full reversal tends to result in repeated activity.
3. Fish are aware of the coastal profile on a kilometre scale and avoid potential expenditures of time and energy in fine-scale manoeuvres by aligning with the coast.
4. Advection by currents is not perceived in the absence of an absolute frame of reference and drift is incorporated in the migratory route.
5. After a variable period of directed activity, random activity and drift, sexually maturing adult fish reach a point from which they begin their homewards migration that is located on a front to the north and west of the UK land-mass, with extremities near the Faroe and Greenland regions.
6. Adults migrate inwards from the ocean with sufficient accuracy to intercept the western UK coastal domain by adopting a heading with a southwards and eastwards bias.
7. Adults limit their tendency to southwards migration in the ocean domain using a latitudinal sense and imprinted information on the latitude of their point of departure from the coast as smolts.
8. On entry to the coastal domain, proximate cues for orientation take precedence over preferred headings.
9. Adult fish of western river origin making landfall north of their home river re-align obliquely to the coast and continue southwards towards the imprinted latitudinal location of the home river.
10. Adult fish of western river origin making landfall south of their river of origin re-orientate northwards using imprinted latitudinal cues for the home river.
11. Adult fish of eastern origin making landfall in the western Scottish domain to the south of a route of passage re-orientate northwards towards the imprinted latitudinal position of their route of passage as smolts. On reaching passage, they re-align to the coast on their preferred south-easterly heading.
12. Adult fish of eastern origin that reach eastwards passage by moving southwards along the coast re-align obliquely to the coast on the preferred south-easterly heading.
13. In the coastal domain, proximate cues for orientation gradually replace the tendency towards an innate heading.
14. In the vicinity of the home river, adults intercept the home river odour plume and move up the odour gradient towards its source.
15. Imprinted latitudinal cues for the home river counter any tendency to overshoot home river locations, and particularly small rivers with small plumes, by limiting southwards movement and causing a northwards return.

In the particular context of renewables developments, the conceptual model raises two potentially notable issues by requiring conditions that cannot be supported by direct evidence:

1. Tagging studies show that adult fish of east coast origin are present in fisheries on the northern coasts of Sutherland and Caithness (Malcolm et al. 2010). The conceptual model requires that, at the smolt stage, such fish must exit the North Sea by way of the Pentland Firth, since they must imprint to its latitude in order to return there as adults.
2. In the particular context of the Pentland Firth, the conceptual model results in salmon returning to east coast rivers spilling round and along the north mainland coast. This arises as a result of acute coastal re-alignment towards the preferred south-easterly heading for those fish that have previously made landfall to the south and oblique re-alignment to the same preferred heading by fish that have made landfall to the north. This pattern is consistent with the absence of historical records of salmon fisheries on the Orkney coasts of the Pentland Firth.

The Pentland Firth is the only route into the North Sea that has been shown to be used by Scottish salmon and the conceptual model accommodates this role. The model also allows fish to reach the east coast via the near-continuum of coasts that links the Orkney Sounds and the north Orkney coast with the southern rivers. However, in the case of potential routes along the coasts of the Shetland Islands, the distance between southern Shetland and the northernmost islands of Orkney (ca. 80 km) is too great to propose continuity in the availability of coastal cues. Under these circumstances, a potential weakness in the model arises from its dependence on the interaction of returning adults with coastal cues to limit eastwards movement. As a result, the model does not allow fish that may use routes around or to the north of Shetland to reach rivers in Scotland.

Routes around the Shetland Islands may well be used by salmon originating in south-west Norway and western Sweden since the islands lie on a direct inwards course from the seas around the Faroe Islands, for example, to the coasts near their home rivers. The geographical patterns of coastal capture documented by Hansen et al (1993) for the Rivers Imsa and Sandvik are consistent with this possibility. However, patterns of return to the Rivers Nidelva and Vefsna, further north, are not consistent with an inwards route lying as far south as Shetland (Fig. 4.2). By extension, the differences evident among Norwegian rivers suggest that the routes for fish returning to Scottish rivers are likely to lie even further

south than those for southern Norway. Indeed, the direct inwards route to any of the Scottish rivers from any starting point at or west of the Faroe Islands does not include the seas to the north of the Orkney Islands (Fig. 4.2). Nevertheless, it would be of particular value to find a way to test the possibility of such a northern route because any salmon using it to reach the Scottish east coast will by-pass renewables development in the Pentland Firth and need not pass other areas of development including, for example, the Moray Firth; a potential means of examining this question is outlined in Chapter 5.

4.12 Strategic research on migratory mechanisms

Two priority areas for future research on migratory mechanisms can be identified:

1. Sand and Karlsen's (2000) hypothesis on the role of sound as a cue for orientation in migrating fish should be tested. Focus would be on the coastal and near-shore zones to examine mechanisms by which smolts and adult salmon may sense the coastal profile to support avoidance of shorelines and real, or *de facto*, coastal alignment during passage. An understanding of coastal acoustic profiles is potentially important in considering any coastal bias in migration routes relative to the location of sites of renewables development, particularly because marine installations generate sound and, in particular, low frequency sound (Wahlberg & Westerberg 2005; Li & Çalişal 2010).
2. The SALSEA-MERGE (2012) database should be extended by using recently developed genetic methods to assign smolts captured in experimental fisheries along the continental shelf edge to their region of origin on a finer geographical scale than at present. It is expected that this approach would solve the crucial need to define an early marine position for smolts originating in the rivers of the Scottish east coast and to establish their frequency among smolts from other locations. This knowledge will support strong inferences on the route of exit of smolts from the North Sea.

Chapter 5. Using tagging data to interpret migratory routes

5.1 Historical studies

The first systematic studies of salmon migration routes on the Scottish coasts, as revealed by tagging, were carried out more than one hundred years ago by W.L. Calderwood, the Inspector of Salmon Fisheries for Scotland. An irregular series of similar studies were subsequently conducted by Salmon Inspectors, including W.J.M. Menzies and others, at various commercial fisheries around the coast.

5.1.1 Adults

All the studies were carried out in the same way by capturing adult salmon at netting stations, marking the fish with numbered tags, releasing them and compiling reports of tags subsequently recovered in fisheries elsewhere. Contemporary data of the same type cannot be obtained because the contraction of the commercial netting industry over the last 30 years has greatly reduced the scope for tagging fish and the likelihood of re-capture. The historical reports span 80 years (Table 5.1) and contain a large number of observations and an inconsistent range of other information such as fish-size and sea-age. Overall, the geographical coverage of the data is extensive. The data are potentially a valuable resource for assessing migratory routes, particularly since other information is lacking. In the past, data treatment has been descriptive only. These historical records have been digitised in an attempt to redress this shortcoming. Reports were carefully examined and all relevant data extracted and compiled into a spreadsheet. In particular, geo-referenced locations were added for each record. Relevant data included only those fish that were subsequently recaptured at some distance from their tagging location, at different locations on the coast or in different rivers (recaptures in the same location or river in which the fish were tagged provide no information about migratory movements). This new digital resource contains almost 1000 records. For example, data from a tagging experiment at Kintradwell in 1915 are shown in Figure 5.1.

Table 5.1 Historical reports containing data on movements by tagged adult salmon.

Year	Author	Title
1901	Calderwood, W.L.	Twentieth annual report to the Fishery Board of Scotland, Appendix II. A contribution to the life history of the salmon, as observed by means of marking adult fish
1903	Calderwood, W.L.	Twenty-second annual report to the Fishery Board of Scotland, Appendix III. A contribution to the life history of the salmon, as observed by means of marking adult fish (second paper).
1905	Calderwood, W.L.	Twenty-fourth annual report to the Fishery Board of Scotland. Appendix II. A contribution to the life history of the salmon, as observed by means of marking adult fish (third paper).
1906	Calderwood, W.L.	Twenty-fifth annual report to the Fishery Board of Scotland, Appendix IV. Salmon marking results.
1907	Calderwood, W.L.	Twenty-sixth annual report to the Fishery Board of Scotland, Appendix II. Results of salmon marking.
1908	Calderwood, W.L.	Twenty-seventh annual report to the Fishery Board of Scotland, Appendix II. Results of salmon marking.
1910	Calderwood, W.L.	Salmon Fisheries 1910 No. II. Results of salmon marking – Seventh paper
1911	Calderwood, W.L.	Salmon Fisheries 1911. Results of salmon marking – Eighth paper
1913	Calderwood, W.L.	Salmon Fisheries 1913 Nos I, II and III (April 1914)
1915	Calderwood, W.L.	Salmon Fisheries 1914 No. III Salmon research in the sea – Sea netting results
1916	Calderwood, W.L.	Salmon Fisheries 1915 No. I. Sea netting results (July 1916)
1921	Calderwood, W.L.	Salmon Fisheries 1921 No. I Salmon research in 1920 – sea netting results
1922	Calderwood, W.L.	Salmon Fisheries 1922 No. I. Results of salmon and sea trout marking in river and sea.
1937	Menzies, W.J.M.	Salmon Fisheries 1937 No. I. The movements of salmon marked in the sea. The North-west coast of Scotland in 1936.
1938	Menzies, W.J.M.	Salmon Fisheries 1938 No. I. The movements of salmon marked in the sea. The west coast of Sutherland in 1937.
1938	Menzies, W.J.M.	Salmon Fisheries 1938 No. VII. The movements of salmon marked in the sea. The island of Soay and Ardnamurchan in 1938.
1985	Shearer, W.M. and Jenkins, D.	The status of Atlantic salmon in Scotland.

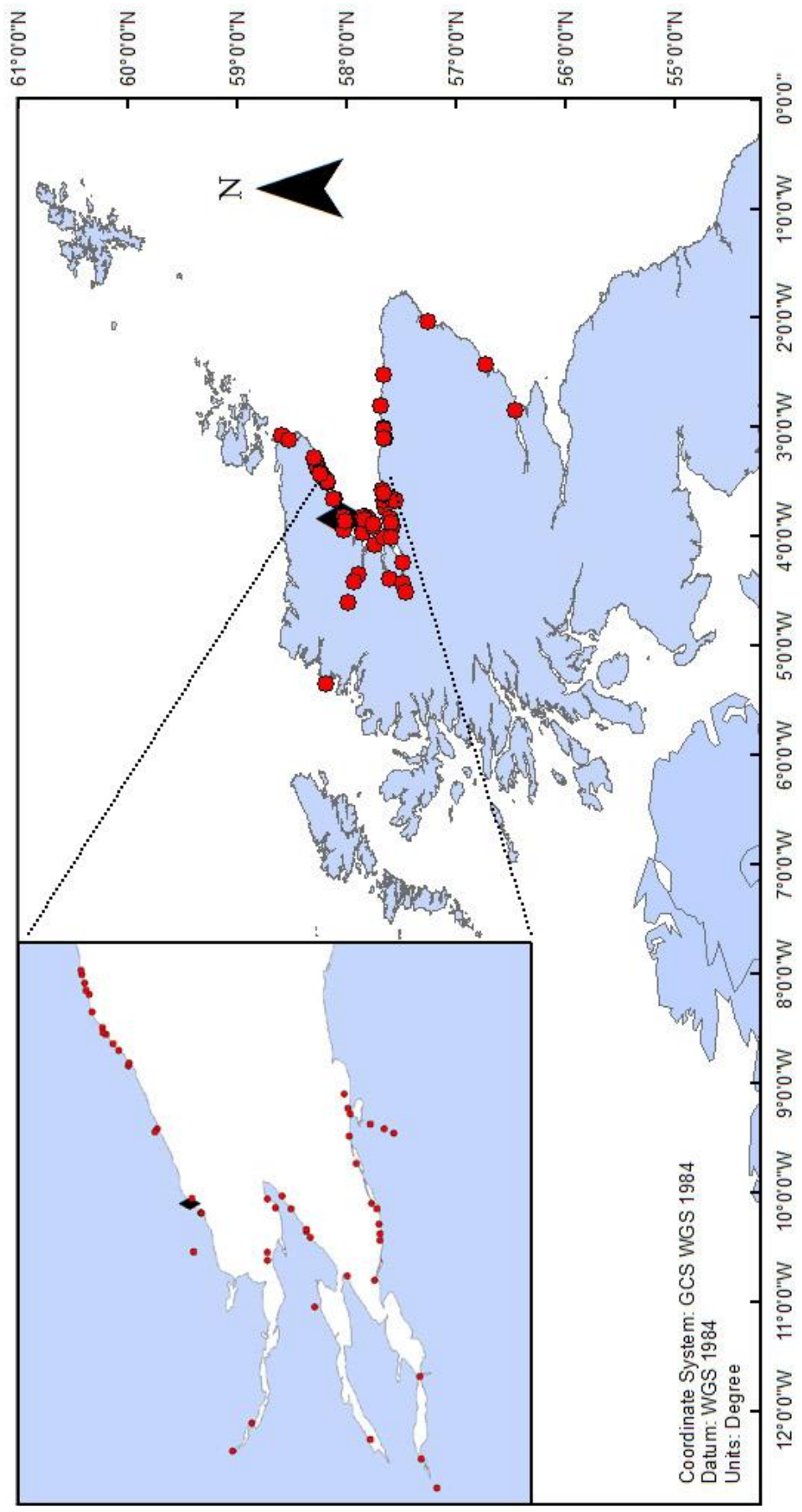


Figure 5.1. Locations (red circles) where 344 adult salmon, tagged at Kintradwell (black diamond) in 1915, were recaptured. From the tagging station, some fish moved south along the coast, whilst others moved north. On smaller-scale maps, the spread of dots indicates the regions or districts in which recaptures occur, without much information about the relative numbers of recaptures in different places. At larger scales (inset), greater detail can be resolved, but since several fish can be caught at a single location, there is not an exact correspondence between the number of circles and the number of fish.

In addition, three similar tagging experiments were carried out on adult salmon along the north coast of Scotland during the late 1970s. These data were provided in digital format by Marine Scotland Science, to which geo-referenced locations have now been added. The amount of data is not large (150 recaptures), but it provides additional information about movements along a key section of coastline (i.e. near the Pentland Firth).

These data, previously unavailable in this form, are now available to develop a fuller understanding of migratory routes. This can be approached in two ways.

1. Visual assessment of patterns of distribution and movement of tagged adult salmon.
2. Numbers of fish caught in different fishery districts could be incorporated in the probabilistic approach described in Section 5.2.

5.1.2 Smolts

In addition to the older tagging experiments using adults, an ambitious programme of tagging smolts as they left their home rivers was established during the late 1960s/early 1970s in a small number of key rivers on the east coast of Scotland. Data on recaptures of adults from some of these programmes (e.g. from the Rivers Tay and N. Esk after 1991) have already been digitised and have been provided by collaborating staff at Marine Scotland Science. Other sets of data were available only as hand-written entries in notebooks (e.g. River N. Esk, pre-1991 and River Dee). All existing records for the River Dee, in addition to data from 1968-70 for the N. Esk, have now been compiled, digitised and geo-referenced. In total, there are over 2100 records with information on location and date of recapture.

Addition of geo-referenced locations is key to this project as it allows records from a range of sources to be plotted in GIS layers and to be allocated to individual fishery districts or combinations of fishery districts. Recaptures of smolts tagged in the River North Esk during 1970 are shown as an example (Figure 5.2).

Copies of these spreadsheets and GIS files will be provided to Marine Scotland Science to supplement their existing database on tagged salmon, and to The Crown Estate and other interested parties.

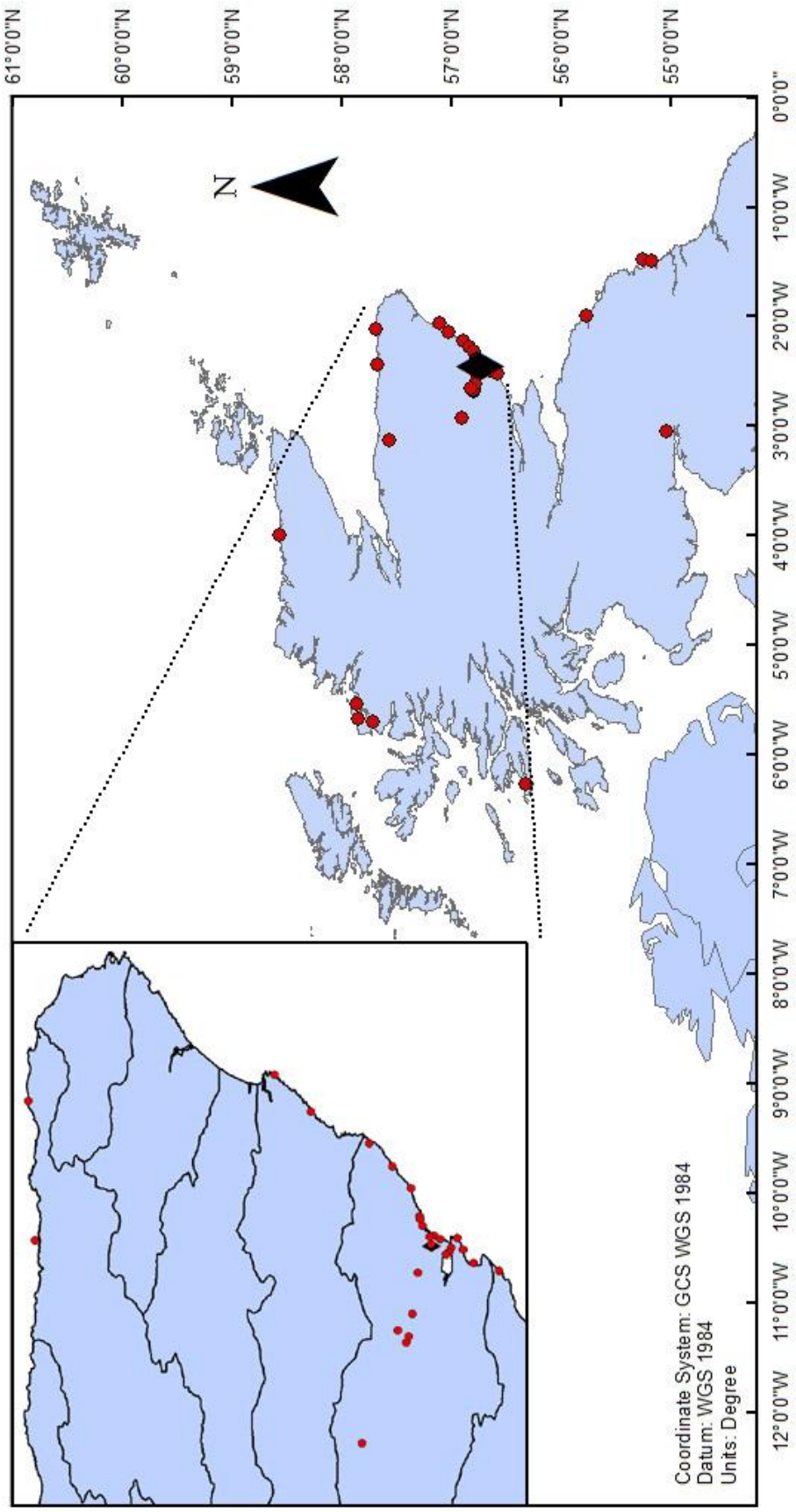


Figure 5.2. Locations (red circles) where 357 adult salmon, tagged as smolts in the River North Esk (black diamond) in 1970, were recaptured. As for Figure 5.1, there is not an exact match between numbers of circles and fish. The inset shows greater detail of locations of recaptures around the home river. Black boundaries represent fishery districts, reproduced by permission of Ordnance Survey on behalf of HMSO © Crown copyright and database right 2012. All rights reserved. Ordnance Survey licence number 100024655.

Visual inspection of such figures has certain merit. It can indicate spatial distributions of returning adults as they head towards their home river. It cannot, however, provide any information about the directions in which the fish were moving. The inability to resolve all individual fish is also a problem. This can be partly overcome by plotting points proportional in size to the numbers of fish caught at that location (e.g. Malcolm et al. 2010), although this can be at the expense of fine-scale resolution of locations (e.g. large circles may obscure smaller ones). The spatial distribution of recaptures can inform interpretations of appropriate spatial domains for hydrodynamic modelling (Chapter 2), of particular behaviours given to particles in tracking models (Chapter 3) and of the mechanisms used during migration (Chapter 4), but additional information is required to derive maximal value from the data. For a probabilistic (rather than a descriptive) understanding of migration, it is also necessary to use the numbers of fish returning to particular places in relation to the number which might have left. In the following section, a novel cellular model is described which can incorporate these data.

5.2 A cellular model of coastal migration of salmon

5.2.1 Historical fisheries

Historically, tagging was carried out at a large number of netting stations at various points around the coast and recaptures were made in considerable numbers. All these fisheries are constant in time because they are defined by property law. Tags were recovered in three main types of fisheries:

1. So-called 'fixed engines' are net traps with a leader net extending shoreward either fixed by anchors or attached to stakes driven into sand beaches. Bag-nets are fished offshore but generally within several hundred meters of land and they are fished by boat. Stake-nets fish across the inter-tidal area on sloping sand beaches and they are tended as the tide recedes. Stake nets fish across a range of up to several hundred metres depending on the gradient of the beach and the phase of the tidal cycle. All the fixed engines operate within about 500m of the shore.
2. So-called 'net-and-coble' fisheries deploy sweep-nets in the lower reaches of rivers or in estuaries.
3. Rod fisheries operate only within rivers.

At the time of the earlier tagging experiments, netting was a major industry and most stations were probably active. However, specific information on uptake, effort or catches is unlikely to have been permanently documented and is certainly not readily available. In 1952, a central system of recording was instituted by which active stations and catches were documented each year and this system has continued to the present. Although active netting units are now few in number, in the earlier years of recording, the system probably captured the industry and the sports fisheries at a stage where fishing effort, and the apportionment of catches among sectors, had been relatively stable for many decades. Therefore, the documented state of the fisheries in the 1950s probably approximates their state over the period when the tagging studies were carried out.

5.2.2 The cellular model

Assuming that the above is correct, fixed-engines around Scotland can be regarded as a temporally stable, linear set of fishery units (represented as dark blue rectangles in Figure 5.3) that potentially sample salmon at random as they return to their river of origin along a coastal route. Thus the null hypothesis is that salmon originating from any river unit (yellow) that are caught, tagged and released (red) in any single specified fixed engine fishery unit (FE 0) will be represented among tagged fish according only to the relative productivity of the river unit in question. Fishery units could correspond to individual fishery districts or amalgamations of districts (the boundaries of which are well established), or to other areas of interest (catchments, regions, counties, etc.). Salmon are assumed to be sampled randomly by the same or any other fixed-engine unit according to their subsequent direction of movement (+ or -) towards the home river unit and the magnitude of the fishing effort (represented by rectangle size) in the series of fixed-engine units distributed along the coast between the point of tagging and the home river unit (R). Tagged fish entering their home river units will be sampled by net-and-coble (NC) or by rod and line (RL) fisheries or they will escape to spawn. Home-river units are represented as a linear series matching the spatial arrangement of the fixed engine units; (river productivity is represented by size of yellow rectangles).

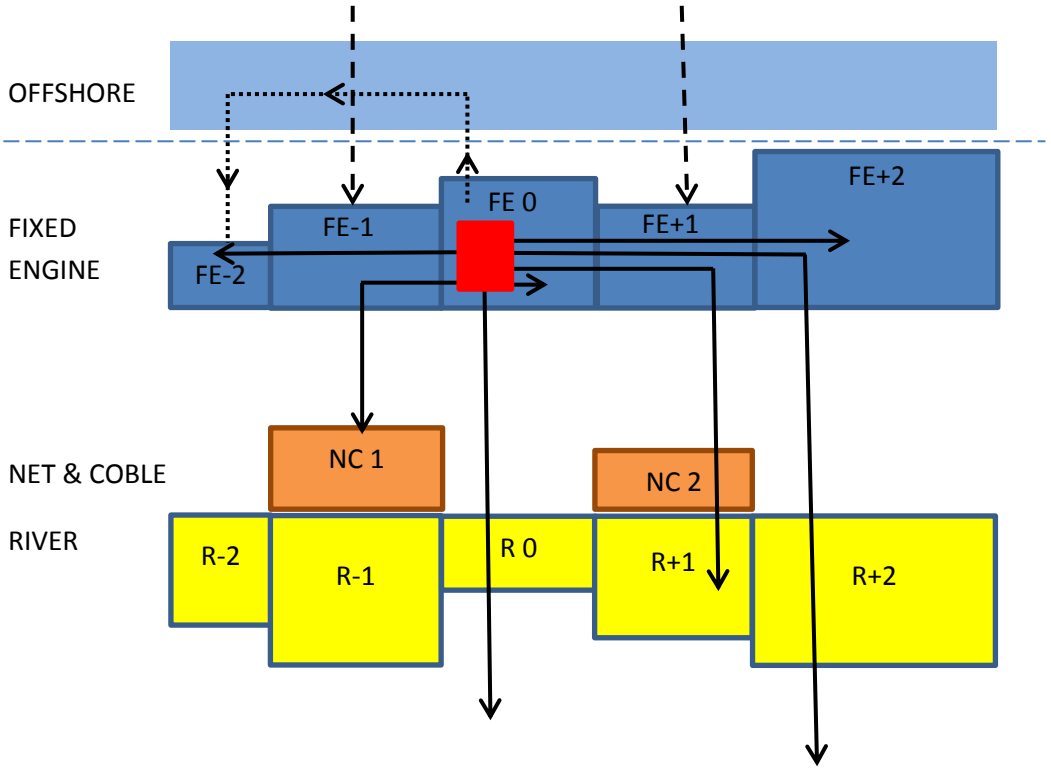


Figure 5.3 Schematic diagram of the cellular model developed here to allow a probabilistic approach to understanding the likelihood of salmon from any given river being caught in a specified fishery, and hence, greater understanding of migratory routes used by returning adult salmon. Yellow cells are river units, where the size of the rectangle represents the numbers of fish produced in that unit. Dark blue cells (coastal fixed-engine fishery units) and orange cells (net and coble fishery units) are associated with each river unit; in each case, the size of the rectangle is proportional to magnitude of fishing effort. Unbroken lines indicate some possible routes and final positions of recaptured or undetected fish. Dashed arrows indicate potential discrete inward routes of fish from the ocean to coastal waters and dotted arrows indicate potential 'short-cuts' taken by salmon through offshore water, by-passing some coastal fisheries.

Considering the river (yellow), net-and-coble (orange - only on some rivers) and fixed engine (dark blue) cells (Figure 5.3):

If fish are sampled randomly, then, for any tagging station (FE 0), the probability (p) that a tagged fish is targeting any particular home river (R_h), is

$$\boldsymbol{pR_h = \frac{PR_h}{\sum PR_i}} \qquad \text{Equation 5.1}$$

where P is the total productivity of R_h, divided by the summed total productivity of all members of the linear series of rivers, R_i.

For this to function, several assumptions have to be made:

1. productivity of a river unit is proportional to catchment area or some better proxy;
2. after tagging, subsequent movement from FE 0 to R_h is unidirectional;

3. after tagging, the probability that the fish will be intercepted en route to its home river is inversely proportional to the combined magnitude of the intervening fisheries;
4. in any river, both NC and RL catches are attributable to that river; and
5. the probability of detection for an individual salmon in any river is proportional to the sum of the yield from NC and RL catch for that river divided by the total productivity for that river.

The model would be populated using:

1. Estimates of productivity of each river unit (e.g. known catchment sizes);
2. Probabilities for tag detection in home rivers across individual tagging experiments (Equation 5.1); and
3. Observed probabilities for recapture in FE (from the tagging datasets).

Observed probabilities for recapture in the fixed-engine units could be compared with calculated expected probabilities of recapture in the home river, for each tagging experiment or dataset. Fishery units can be amalgamated to any extent required by the limitations imposed by the combined size of the data sets.

It is anticipated that the null hypothesis (salmon originating from any river unit that are caught, tagged and released in any single fixed engine fishery unit will be represented among recaptured fish according to the relative productivity of that river unit) will not be supported. This is primarily due to the assumption that fish return randomly from the ocean to FE units, which is likely to be an over-simplification. Outputs from the cellular model of greatest interest and value in the context of this report include:

1. geographical (locational) discontinuities in probability values. Such discontinuities may indicate locations of different discrete inputs of fish from the ocean destined for particular rivers (or more probably, to groups of contiguous catchments), for example, discrete inputs from the ocean, say, to Cape Wrath and / or to Kinnaird Head (Figure 5.3, dashed black lines);
2. geographical (locational) discontinuities in probability values that may indicate exiting/re-entering of fish from/to coastal waters as they take ‘short-cuts’ through offshore waters (rather than following the coast), bypassing some coastal fisheries as they do so (Figure 5.3, dotted black lines). For example, fish might cross the outer Moray Firth rather than following the coast-line through the fisheries); and
3. behaviours local to fisheries such as inconstancy in directionality or over-representation of fish in the proximity of their home rivers, which can then be recognised and compensated for when parameterising PTMs.

The next step in this approach will be to apply historical data to this cellular model for Scotland. Data in hand-written note-books also exist for the North Esk from other years in the 1970s and 80s. Application of the digitised early data for this river (1968-70) to the cellular model will provide an interesting comparison to later data (post-1991). Such comparisons may indicate whether or not there is additional information to be gained from the effort required to digitise and geo-reference the remaining notebooks.

Such an approach, giving a probabilistic understanding of migratory routes taken by Atlantic salmon, has great potential for improving our knowledge of salmon ecology, for defining more precise hypotheses to be tested by field- or computer-based studies, and for the obvious value, derived through numerical modelling, of a better understanding of risks to salmon from marine developments. The cellular model continues to be developed, populated and tested with different combinations of data, but these are in a preliminary state and not within the scope of this report.

Chapter 6. Conclusions

The main purpose of this report has been to evaluate the potential use of biologically parameterised particle-tracking models (PTMs) to assess the likelihood that migratory salmon may pass through areas of interest for marine developments. The preceding chapters have demonstrated that the hydrodynamic modelling approach is technically feasible, but that there are outstanding challenges relating, in particular, to the selection of biological parameter values. Particle 'swimming' speeds can probably be applied with some confidence for both adult and juvenile salmon using values from the literature. However, the question of directed activity cannot be addressed in the same way since there is very little empirical information on orientation at any stage of migration, particularly in dynamic regimes such as the Pentland Firth. Moreover, although the starting and final positions of fish can be assumed to be the home river, their intervening positions and timings are also generally unknown. As a result, there is currently no basis on which to feed particles (numbers, river origin, entry timing or entry position) into models run on any scale that does not include the river of origin.

To address these problems, a conceptual model (Section 4.11) has been developed that constrains fish to conform to observed patterns of dispersal by making a minimal number of, arguably plausible, assumptions based on interpretation of the research literature on migration in salmonids and other species. The aim of this approach is to capture a plausible set of dominant mechanisms that determine patterns of migration, particularly in the coastal phases. This, or a similar construct, may ultimately prove to be informative for parameterising PTMs carried out on broader scales, although such a structure is unlikely to capture the detail relevant to finer spatial or temporal scales. In addition, the construct is partly based on an informal understanding of the patterns of dispersal observed in previous tagging studies (Malcolm et al. 2010), meaning that the same studies cannot be used to test the construct.

Biological data remain limiting and any attempt at modelling will be constrained by the lack of direct, observational information on the activity and dispersal of migrants at both the smolt and adult stages. Any modelling will therefore need to be coupled with sensitivity analyses, in order to explore the effects of uncertainty in parameter estimation.

Consideration of smaller, and therefore slower-swimming, fish is likely to prove more robust than consideration of large fish, assuming that the effects of large uncertainties in the biological parameters of the PTM are buffered by lower levels of uncertainty in the hydrodynamic parameters. This will be especially the case for small fish in highly dynamic environments where net movement is likely to be dominated by the effects of advection rather than by fish activity (i.e. the fish will more closely resemble passive particles). All these conditions can be met, for example, for smolts from Thurso River moving within a robust PTM simulation of the Pentland Firth lasting only over several tides.

Given the current absence of competing options, it will probably be considered justifiable to run biologically-parameterised PTMs along the lines described above. In the particular case of the Pentland Firth, the PTM approach may be considered for adult passage since current velocities frequently approach or exceed the putative swimming speeds of large fish. In the case of the Moray Firth (for example), the PTM approach to modelling adult movement may prove less informative since model output will be dominated by uncertainties in the behavioural parameters ascribed to the fish rather than by the hydrodynamic content of the model.

The latter case highlights the necessity of gaining a better understanding of migratory behaviours like those incorporated in the conceptual model developed in this report. The most rapid advances in this area will probably be gained through field experimentation and observation since many of the relevant mechanisms have already been identified. Furthermore, migration and navigation are vigorous fields of investigation as evidenced by the large number of very recent reports on many species cited in the present document. Future insights derived from such studies can be incorporated into a revised conceptual model like the one developed here, acknowledging that the lack of direct evidence means that the present model must be regarded as provisional.

The conceptual model, or an alternative structure, can act as a basis for formulating hypotheses and identifying, prioritising and targeting the most important knowledge gaps. If some of these gaps can be filled, it may become possible for the first time to address a set of important questions. For example, it may be possible to discover whether all fish from all the Scottish east coast rivers use the Pentland Firth for access to and from the North

Atlantic or whether some fish use a route east of Orkney. It may be possible to discern whether fish using the Pentland Firth for passage are uniformly distributed across its width or whether the Inner Sound of Stroma (for example) is a preferred route. It may be possible to find out whether fish originating south of the Moray Firth follow the coastline of the Inner Firth or whether they cross directly from near Kinnaird Head to Duncansby Head. None of these questions can be answered at present, but all of them are directly relevant. Furthermore, a broad scale understanding of the migratory routes of fish from different rivers or regions will facilitate PTMs implemented on local scales by providing realistic inputs for some or all of the missing variables identified above (i.e. fish numbers, river of origin, entry timing and entry position). Developing this capacity would ensure a state of readiness to further refine PTMs in the light of any new data. In addition, operational hydrodynamic models would provide a template for the interpretation of any future work designed to determine swimming speeds and orientation from experimental observations of net displacement, by distinguishing the effects of advection from those of swimming activity.

Following on from this, there are several well-defined projects that could reasonably be expected to provide important information quickly and which could be implemented without delay.

1. The cellular model (Chapter 5) could be parameterised with fishery data and implemented to attempt a probabilistic interpretation of the historical data derived from tagging and recapture of adult fish. This may identify discontinuities in the migratory paths of adults returning to different rivers or to different regional river groupings. For example, it may show that adults from the large, south-eastern Scottish rivers were under-represented in the northern fisheries where tagging was carried out (e.g. in the Pentland Firth). If so, this will imply that inwards routes differ for fish returning to different rivers or different regional groupings. Historical tagging data represent a unique resource that offers (via the cellular model) perhaps the best available approach to exploring these issues, since the contraction of the netting sector precludes any attempt at replicating the historical work.
2. A refined, high-resolution PTM could be implemented to simulate the trajectories of smolts and adult salmon passing through the Pentland Firth. This should ideally be based on existing hydrodynamic models which have already been created for resource assessment and other purposes (detailed recommendations can be found in Section 2.5.1).

3. A larger-scale PTM could be implemented to explore the migratory mechanisms of Atlantic salmon on the basis of the conceptual model outlined in Chapter 4. This could follow on from work conducted under the SALSEA-MERGE programme (Mork et al. 2012).
4. Similar exercises, using intermediate-scale models, could be carried out to explore the trajectories taken by outmigrating smolts, particularly from the rivers of the east coast and Moray Firth, to determine the likelihood that smolts from these rivers pass through the Pentland Firth (or other areas) during the early stages of their oceanic migration.
5. The genetic samples collected west of the Hebrides and in the southern Norwegian Sea in the course of the SALSEA-MERGE project should be re-analysed, using an improved set of genetic markers, to identify any smolts originating from eastern Scottish rivers. This work would be expected to establish whether smolts from the large and productive eastern rivers exit the North Sea via a southern route (the Pentland Firth/ Orkney Sounds) or via an eastern route through the northern North Sea.
6. The conceptual model of migration presented in this report is restricted in scale to the Scottish coastal area. Its robustness should be considered and tested on a wider geographical scale to determine whether it can account for observed fish movements to and from rivers set in a wider range of geographical settings. If necessary, a refined version of the Scottish model should be constructed to act as an improved template for the formulation and testing of hypotheses on migratory mechanisms.

More generally, there is a pressing need for observational studies of fish movement in various stages of the coastal migration of both smolts and adult salmon. Data on the activity, orientation and movement of individuals in Scottish waters are an obvious requirement for developing useful particle-tracking models for areas such as the Pentland Firth. Equally, however, data for movement toward and into such areas for fish originating over the range of river origins are required to provide numbers and locations of fish for input into high-resolution simulations. There are two categories of approach to obtaining these types of data. First, a direct observational approach can be based, for example, on acoustic or data-logging tags, including pop-up tags. Second, an indirect approach is possible based on genetic characterisation of sampled fish, particularly if the level of genetic discrimination can be improved to identify river of origin in mixed samples of fish.

In final conclusion, hydrodynamic models appear to offer the best available approach to answering some of the questions regarding the passage of migratory fish through areas where marine developments may take place. Although the overall approach is constrained by lack of biological knowledge, modelling is likely to produce informative output over an important range of definable contexts, as outlined above. These outputs are likely to be of immediate value to a diverse set of stakeholders, including technology developers, conservation agencies and regulators. Furthermore, any new biological insights will tend to strengthen the modelling approach and extend the range of contexts to which it can be applied with confidence. An active programme of model development, application and assessment will inform biological data gathering and will ensure a state of readiness to incorporate new insights without delay.

ACKNOWLEDGEMENTS

The authors are grateful to The Crown Estate for funding the project. AJ was also supported by funds from the Highlands and Islands Enterprise, the Scottish Funding Council and the European Regional Development Fund through the Marine Renewable Energy and the Environment (MaREE) programme. We also thank Professor Stuart Gibb and Jacqueline Black for institutional support during the initiation of the project.

The section on historical data would not have been possible without the cooperation of Marine Scotland Science. MSS staff provided invaluable assistance with the identification and provision of reports on salmon tagging studies in Scottish waters, as well as access to other relevant data, and many useful discussions on the scope of this project. In particular, the authors thank Jason Godfrey, Stuart Middlemas, Julian MacLean and Gordon Smith.

In addition, the authors thank Astrid Harendza, Jill Noble, Hester Jackson, Paul Gaffney and Barbara Bremner for their hard work on the transcription and geo-referencing of historical salmon tagging data.

Philippe Gleizon reviewed Chapter 2 and provided many helpful comments.

REFERENCES

Abascal, A. J., S. Castanedo, V. Fernández and R. Medina. 2012. Backtracking drifting objects using surface currents from high-frequency (HF) radar technology. Ocean Dynamics **62**: 1073–1089.

Able, K. P. and M. A. Able. 1996. The flexible migratory orientation system of the savannah sparrow. Journal of Experimental Biology **199**: 3–8.

ABPmer. 2008. Atlas of UK Marine Renewable Energy Resources. Date Accessed: 13-Mar-2013. http://www.renewables-atlas.info.

Adlandsvik, B., A. C. Gunderder, K. H. Nedreaas, A. Stene and O. T. Albert. 2004. Modelling the advection and diffusion of eggs and larvae of Greenland halibut (*Reinhardtius hippoglossoides*) in the north-east Arctic. Fisheries Oceanography **13**: 403–415.

Alerstam, T. 2006. Conflicting evidence about long-distance animal navigation. Science **313**: 791–4.

Aster, R. C., D. E. McNamara and P. D. Bromirski. 2008. Multidecadal Climate-induced Variability in Microseisms. Seismological Research Letters **79**: 194–202.

Ayata, S.-D., P. Lazure and É. Thiébaut. 2010. How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (North-East Atlantic). Progress in Oceanography **87**: 18–36.

Azumaya, T. and Y. Ishida. 2004. An evaluation of the potential influence of SST and currents on the oceanic migration of juvenile and immature chum salmon (*Oncorhynchus keta*) by a simulation model. Fisheries Oceanography **13**: 10–23.

Bacon, P. J., S. C. F. Palmer, J. C. MacLean, G. W. Smith, B. D. M. Whyte, W. S. C. Gurney and A. F. Youngson. 2009. Empirical analyses of the length, weight, and condition of adult Atlantic salmon on return to the Scottish coast between 1963 and 2006. ICES Journal of Marine Science **66**: 844–859.

Bardyshev, V. I. 2008. Underwater surf noise near sea coasts of different types. Acoustical Physics **54**: 814–822.

Baston, S. and R. E. Harris. 2011. Modelling the Hydrodynamic Characteristics of Tidal Flow in the Pentland Firth. *9th European Wave and Tidal Energy Conference*. Southampton, UK.

Batchelder, H. P. 2006. Forward-in-Time-/Backward-in-Time-Trajectory (FITT/BITT) Modeling of Particles and Organisms in the Coastal Ocean. Journal of Atmospheric and Oceanic Technology **23**: 727–741.

Baxter, J. M., I. L. Boyd, M. Cox, A. E. Donald, S. J. Malcolm, H. Miles, B. Miller, C. F. Moffat and (Editors). 2011. Scotland's Marine Atlas: Information for the national marine plan. Marine Scotland, Edinburgh. Edinburgh.

Berthold, P. and A. J. Helbig. 1992. The genetics of bird migration: stimulus, timing, and direction. Ibis **134 Suppl**: 35–40.

Berthold, P., A. J. Helbig, G. Mohr and U. Querner. 1992. Rapid microevolution of migratory behaviour in a wild bird species. Nature **360**: 668–670.

Berthold, P. and U. Querner. 1981. Genetic basis of migratory behavior in European warblers. Science **212**: 77–79.

Bingman, V. P. and K. Cheng. 2005. Mechanisms of animal global navigation: comparative perspectives and enduring challenges. Ethology Ecology & Evolution **17**: 295–318.

Bonhommeau, S., B. Blanke, A. Tréguier, N. Grima, E. Rivot, Y. Vermard, E. Greiner and O. Le Pape. 2009. How fast can the European eel (*Anguilla anguilla*) larvae cross the Atlantic Ocean? Fisheries Oceanography **18**: 371–385.

Booker, D. J., N. C. Wells and I. P. Smith. 2008. Modelling the trajectories of migrating Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **65**: 352–361.

Boström, J. E., S. Åkesson and T. Alerstam. 2012. Where on earth can animals use a geomagnetic bi-coordinate map for navigation? Ecography **35**: 1039–1047.

Bourque, M.-C., P. H. LeBlond and P. F. Cummins. 1999. Effects of tidal currents on Pacific salmon migration: results from a fine-resolution coastal model. Canadian Journal of Fisheries and Aquatic Sciences **56**: 839–846.

Bracis, C. and J. J. Anderson. 2012. An investigation of the geomagnetic imprinting hypothesis for salmon. Fisheries Oceanography **21**: 170–181.

Brickman, D., B. Adlandsvik, U. H. Thygesen, C. Parada, K. Rose, A. J. Hermann and K. Edwards. 2009. Particle Tracking, p. 9–19. *In* E.W. North, A. Galleg, and P. Petitgas [eds.], Manual of recommended practices for modelling physical-biological interactions during fish early life. ICES Cooperative Research Report No. 295.

Burke, B. J., M. C. Liermann, D. J. Teel and J. J. Anderson. 2013. Environmental and geospatial factors drive juvenile Chinook salmon distribution during early ocean migration. Canadian Journal of Fisheries and Aquatic Sciences **70**: 1167–1177.

Chaput, G. 2012. Overview of the status of Atlantic salmon (Salmo salar) in the North Atlantic and trends in marine mortality. ICES Journal of Marine Science **69**: 1538–1548.

Chew, G. L. and G. E. Brown. 1989. Orientation of rainbow trout (*Salmo gairdneri*) in normal and null magnetic fields. Canadian Journal of Zoology **67**: 641–643.

Cho, S. and J. W. Choi. 2009. Measurements of breaking wave noise in the sea-cliff zone. **30**: 169–170.

Codling, E. A., M. J. Plank and S. Benhamou. 2008. Random walk models in biology. Journal of the Royal Society, Interface **5**: 813–34.

Corell, H., P. Moksnes, A. Engqvist, K. Döös and P. Jonsson. 2012. Depth distribution of larvae critically affects their dispersal and the efficiency of marine protected areas. Marine Ecology Progress Series **467**: 29–46.

Crossin, G. T., S. G. Hinch, S. J. Cooke, D. W. Welch, S. D. Batten, D. A. Patterson, G. Kraak, J. M. Shrimpton and A. P. Farrell. 2007. Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river. Marine Biology **152**: 905–918.

Dadswell, M. J., A. D. Spares, J. M. Reader and M. J. W. Stokesbury. 2010. The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the "Merry-Go-Round" hypothesis. Journal of Fish Biology **77**: 435–467.

Davies, A. M., P. Hall, M. J. Howarth and P. Knight. 2002. Modelling and measuring the wind forced inflow to the Irish Sea through the North Channel. Continental Shelf Research **22**: 749–777.

DECC. 2012. UK Renewable Energy Roadmap Update 2012. URN 12D/479. Department of Energy and Climate Change. 67pp.

Díaz, B., A. Pavón and M. Gómez-Gesteira. 2008. Use of a probabilistic particle tracking model to simulate the Prestige oil spill. Journal of Marine Systems **72**: 159–166.

Domingues, C. P., R. Nolasco, J. Dubert and H. Queiroga. 2012. Model-derived dispersal pathways from multiple source populations explain variability of invertebrate larval supply. PLoS ONE **7**: e35794.

Dukes, J. P., R. Deaville, D. Gottelli, J. E. Neigel, M. W. Bruford and W. C. Jordan. 2006. Isolation and characterisation of main olfactory and vomeronasal receptor gene families from the Atlantic salmon (*Salmo salar*). Gene **371**: 257–67.

Easton, M. C., D. K. Woolf and P. A. Bowyer. 2012. The dynamics of an energetic tidal channel, the Pentland Firth, Scotland. Continental Shelf Research **48**: 50–60.

Eder, S. H. K., H. Cadiou, A. Muhamad, P. A. McNaughton, J. L. Kirschvink and M. Winklhofer. 2012. Magnetic characterization of isolated candidate vertebrate magnetoreceptor cells. Proceedings of the National Academy of Sciences of the United States of America **109**: 12022–7.

Elliott, A. J., B. T. Wilkins and P. Mansfield. 2001. On the disposal of contaminated milk in coastal waters. Marine Pollution Bulletin **42**: 927–34.

Enger, P. S., H. E. Karlsen, F. R. Knudsen and O. Sand. 1993. Detection and reaction of fish to infrasound. ICES Marine Science Symposium **196**: 108–112.

Flamarique, I. N. and C. W. Hawryshyn. 1997. Is the use of underwater polarized light by fish restricted to crepuscular time periods? Vision research **37**: 975–89.

Fossette, S., N. F. Putman, K. J. Lohmann, R. Marsh and G. Hays. 2012. A biologist's guide to assessing ocean currents: a review. Marine Ecology Progress Series **457**: 285–301.

Fringer, O. B., J. C. McWilliams and R. L. Street. 2006. A new hybrid model for coastal simulations. Oceanography **19**: 64–77.

Furevik, T. 2000. On Anomalous Sea Surface Temperatures in the Nordic Seas. Journal of Climate **13**: 1044–1053.

Gao, Y., H. Drange, M. Bentsen and O. M. Johannessen. 2004. Simulating transport of non-Chernobyl ^{137}Cs and ^{90}Sr in the North Atlantic-Arctic region. Journal of Environmental Radioactivity **71**: 1–16.

Garcia de Leaniz, C., I. A. Fleming, S. Einum, E. Verspoor, W. C. Jordan, S. Consuegra, N. Aubin-Horth, D. Lajus, B. H. Letcher, A. F. Youngson, J. H. Webb, L. A. Vollestad, B. Villanueva, A. Ferguson and T. P. Quinn. 2007. A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. Biological Reviews **82**: 173–211.

Gaspar, P., S. Benson, P. Dutton, A. Réveillère, G. Jacob, C. Meetoo, a Dehecq and S. Fossette. 2012. Oceanic dispersal of juvenile leatherback turtles: going beyond passive drift modeling. Marine Ecology Progress Series **457**: 265–284.

Gaston, T. F., T. A. Schlacher and R. M. Connolly. 2006. Flood discharges of a small river into open coastal waters: Plume traits and material fate. Estuarine, Coastal and Shelf Science **69**: 4–9.

Government, S. 2012. 2020 Renewable Routemap for Scotland - Update. http://www.scotland.gov.uk/Resource/0040/00406958.pdf. 49pp.

Gräwe, U. 2011. Implementation of high-order particle-tracking schemes in a water column model. Ocean Modelling **36**: 80–89.

Greenberg, D. A., F. Dupont, F. H. Lyard, D. R. Lynch and F. E. Werner. 2007. Resolution issues in numerical models of oceanic and coastal circulation. Continental Shelf Research **27**: 1317–1343.

Guizien, K., T. Brochier, J. Duchêne, B. Koh and P. Marsaleix. 2006. Dispersal of *Owenia fusiformis* larvae by wind-driven currents: turbulence, swimming behaviour and mortality in a three-dimensional stochastic model. Marine Ecology Progress Series **311**: 47–66.

Hamann, M., A. Grech, E. Wolanski and J. Lambrechts. 2011. Modelling the fate of marine turtle hatchlings. Ecological Modelling **222**: 1515–1521.

Hansen, L. P., K. B. Doving and B. Jonsson. 1987. Migration of farmed adult Atlantic salmon with and without olfactory sense, released on the Norwegian coast. Journal of Fish Biology **30**: 713–721.

Hansen, L. P., K. D. Friedland, M. Holm, J. C. Holst and J. A. Jacobsen. 2002. Temporal and Spatial Migration and Distribution of Atlantic Salmon, *Salmo salar* L ., in the Northeast Atlantic Ocean. NPAFC Technical Report No. 4.

Hansen, L. P. and J. A. Jacobsen. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. ICES Journal of Marine Science **60**: 110–119.

Hansen, L. P. and B. Jonsson. 1991. Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. Journal of Fish Biology **38**: 251–258.

Hansen, L. P., N. Jonsson and B. Jonsson. 1993. Oceanic migration in homing Atlantic Salmon. Animal Behaviour **45**: 927–941.

Hansen, L. P. and A. F. Youngson. 2010. Dispersal of large farmed Atlantic salmon, *Salmo salar*, from simulated escapes at fish farms in Norway and Scotland. Fisheries Management and Ecology **17**: 28–32.

Harden Jones, F. R. 1968. Fish Migration. Edward Arnold. London, UK.

Harden Jones, F. R., G. P. Arnold, M. Greer Walker and P. Scholes. 1979. Selective tidal stream transport and the migration of plaice (*Pleuronectes platessa* L.) in the southern North Sea. ICES Journal of Marine Science **38**: 331–337.

Hasler, A. D. and W. J. Wisby. 1951. Discrimination of Stream Odors by Fishes and Its Relation to Parent Stream Behavior. The American Naturalist **85**: 223–238.

Haugan, P. M., G. Evensen, J. A. Johannessen, O. M. Johannessen and L. H. Pettersson. 1991. Modeled and Observed Mesoscale Circulation and Wave-Current Refraction During the 1988 Norwegian Continental Shelf Experiment. Journal of Geophysical Research **96**: 10,487–10,506.

Hawkins, A. D. and A. D. F. Johnstone. 1978. The hearing of the Atlantic Salmon, Salmo salar. Journal of Fish Biology **13**: 655–673.

Hays, G. C., S. Fossette, K. A. Katselidis, P. Mariani and G. Schofield. 2010. Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. Journal of the Royal Society, Interface **7**: 1319–27.

Healey, M. C., K. A. Thomson, P. H. Leblond, L. Huato, S. G. Hinch and C. J. Walters. 2000. Computer simulations of the effects of the Sitka eddy on the migration of sockeye salmon returning to British Columbia. Fisheries Oceanography **9**: 271–281.

Heath, M. R. and A. Gallego. 1998. Bio-physical modelling of the early life stages of haddock, *Melanogrammus aeglefinus*, in the North Sea. Fisheries Oceanography **7**: 110–125.

Hellinger, J. and K.-P. Hoffmann. 2009. Magnetic field perception in the rainbow trout, *Oncorhynchus mykiss*. Journal of Comparative Physiology A **195**: 873–9.

Herbert, R. J. H., J. Willis, E. Jones, K. Ross, R. Hübner, J. Humphreys, A. Jensen and J. Baugh. 2012. Invasion in tidal zones on complex coastlines: modelling larvae of the non-native Manila clam, *Ruditapes philippinarum*, in the UK. Journal of Biogeography **39**: 585–599.

Herbert-Read, J. E., S. Krause, L. J. Morrell, T. M. Schaerf, J. Krause and A. J. W. Ward. 2013. The role of individuality in collective group movement. Proceedings of the Royal Society B **280**: 20122564.

Hermann, A. J., D. B. Haidvogel, E. L. Dobbins and P. J. Stabeno. 2002. Coupling global and regional circulation models in the coastal Gulf of Alaska. Progress in Oceanography **53**: 335–367.

Hill, A. E., K. J. Horsburgh, R. W. Garvine, P. A. Gillibrand, G. Slesser, W. R. Turrell and R. D. Adams. 1997. Observations of a Density-driven Recirculation of the Scottish Coastal Current in the Minch. Estuarine, Coastal and Shelf Science **45**: 473–484.

Hill, A. E. and J. H. Simpson. 1988. Low-frequency Variability of the Scottish Coastal Current Induced by Along-shore Pressure Gradients. Estuarine, Coastal and Shelf Science **27**: 163–180.

Hinckley, S., A. J. Hermann and B. A. Megrey. 1996. Development of a spatially explicit, individual-based model of marine fish early life history. Marine Ecology Progress Series **139**: 47–68.

Holm, M. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. ICES Journal of Marine Science **57**: 955–964.

Holm, M., J. C. Holst, L. P. Hansen, J. A. Jacobsen, N. O'Maoileidigh and A. Moore. 2003. Migration and distribution of Atlantic salmon post-smolts in the North Sea and north-east Atlantic, p. 7–23. *In* D. Mills [ed.], Salmon at the Edge. Blackwell Science. Oxford.

Holst, J. C., R. G. J. Shelton, M. Holm and L. P. Hansen. 2000. Distribution and possible migration routes of post-smolt Atlantic salmon in the NE Atlantic, *In* D. Mills [ed.], The Ocean Life of Salmon. Fishing News Books. Blackwell Science Ltd. Oxford.

Huang, W. G., A. P. Cracknell and R. A. Vaughan. 1993. Satellite Thermal Observations of the River Shannon Plume. Estuarine, Coastal and Shelf Science **36**: 207–219.

Huijbers, C. M., I. Nagelkerken, P. A. C. Lössbroek, I. E. Schulten, A. Siegenthaler, M. W. Holderied and S. D. Simpson. 2012. A test of the senses: Fish select novel habitats by responding to multiple cues. Ecology **93**: 46–55.

ICES. 2012. North Atlantic salmon stocks. Report of the ICES Advisory Committee. Agenda Item 5.4.

Isobe, A., S. Kako, P.-H. Chang and T. Matsuno. 2009. Two-Way Particle-Tracking Model for Specifying Sources of Drifting Objects: Application to the East China Sea Shelf. Journal of Atmospheric and Oceanic Technology **26**: 1672–1682.

Jacobsen, J. A., L. P. Hansen, V. Bakkestuen, R. Halvorsen, D. G. Reddin, J. White, N. O'Maoileidigh, I. C. Russell, E. C. E. Potter, M. Fowler, G. W. Smith, K. A. Mork, A. Isaksson, S. Oskarsson, L. Karlsson and S. Pedersen. 2012. Distribution by origin and sea age of Atlantic salmon (*Salmo salar*) in the sea around the Faroe Islands based on analysis of historical tag recoveries. ICES Journal of Marine Science **69**: 1598–1608.

Jensen, J. M. and W. H. Lear. 1980. Atlantic Salmon Caught in the Irminger Sea and at East Greenland. Journal of Northwest Atlantic Fishery Science **1**: 55–64.

Johnson, S. P. and D. E. Schindler. 2012. Marine trophic diversity in an anadromous fish is linked to its life-history variation in fresh water. Biology Letters **9**, doi:10.1098/rsbl.2012.0824

Johnstone, K. A., K. P. Lubieniecki, B. F. Koop and W. S. Davidson. 2012. Identification of olfactory receptor genes in Atlantic salmon *Salmo salar*. Journal of Fish Biology **81**: 559–75.

Jones, J. E. and A. M. Davies. 2001. Influence of Wave-current Interaction, and High Frequency Forcing upon Storm Induced Currents and Elevations. Estuarine, Coastal and Shelf Science **53**: 397–413.

Jonsson, B., N. Jonsson and L. P. Hansen. 2003. Atlantic salmon straying from the River Imsa. Journal of Fish Biology **62**: 641–657.

Jonsson, N., B. Jonsson and L. P. Hansen. 1990. Partial segregation in the timing of migration of Atlantic salmon of different ages. Animal Behaviour **40**: 313–321.

Kako, S., A. Isobe, S. Magome, H. Hinata, S. Seino and A. Kojima. 2011. Establishment of numerical beach-litter hindcast/forecast models: an application to Goto Islands, Japan. Marine Pollution Bulletin **62**: 293–302.

Karcher, M. J., S. Gerland, I. H. Harms, M. Iosjpe, H. E. Heldal, P. J. Kershaw and M. Sickel. 2004. The dispersion of ^{99}Tc in the Nordic Seas and the Arctic Ocean: a comparison of model results and observations. Journal of Environmental Radioactivity **74**: 185–98.

Kedar, S. and F. H. Webb. 2005. The ocean's seismic hum. Science **307**: 682–683.

Kemp, P. S., M. H. Gessel and J. G. Williams. 2008. Response of downstream migrant juvenile Pacific salmonids to accelerating flow and overhead cover. Hydrobiologia **609**: 205–217.

Kershaw, P. J., H. E. Heldal, K. A. Mork and A. L. Rudjord. 2004. Variability in the supply, distribution and transport of the transient tracer ^{99}Tc in the NE Atlantic. Journal of Marine Systems **44**: 55–81.

Kershaw, P. J., R. J. Pentreath, D. S. Woodhead and G. J. Hunt. 1992. A review of radioactivity in the Irish Sea. A report prepared for the Marine Pollution Monitoring Management Group. Aquatic Environment Monitoring Report, MAFF Directorate of Fisheries Research **32**: 65 pp.

Kettle, A. J. and K. Haines. 2006. How does the European eel (*Anguilla anguilla*) retain its population structure during its larval migration across the North Atlantic Ocean? Canadian Journal of Fisheries and Aquatic Sciences **63**: 90–106.

Kim, H., S. Kimura, A. Shinoda, T. Kitagawa, Y. Sasai and H. Sasaki. 2007. Effect of El Niño on migration and larval transport of the Japanese eel (*Anguilla japonica*). ICES Journal of Marine Science **64**: 1387–1395.

Kimura, S., K. Döös and A. C. Coward. 1999. Numerical simulation to resolve the issue of downstream migration of the Japanese eel. Marine Ecology Progress Series **186**: 303–306.

Kingsford, M. J., J. M. Leis, A. Shanks, K. C. Lindeman, S. G. Morgan and J. Pineda. 2002. Sensory environments, larval abilities and local self-recruitment. Bulletin of Marine Science **70**: 309–340.

Knudsen, F. R., P. S. Enger and O. Sand. 1992. Awareness reactions and avoidance responses to sound in juvenile Atlantic salmon, *Salmo salar* L. Journal of Fish Biology **40**: 523–534.

Knudsen, V. O., R. S. Alford and J. W. Emling. 1948. Underwater ambient noise. Journal of Marine Science **7**: 410–429.

Kuang, L., A. F. Blumberg and N. Georgas. 2012. Assessing the fidelity of surface currents from a coastal ocean model and HF radar using drifting buoys in the Middle Atlantic Bight. Ocean Dynamics **62**: 1229–1243.

Lacroix, G., P. McCloghrie, M. Huret and E. W. North. 2009. Hydrodynamic models, p. p3–8. *In* E.W. North, A. Gallego, and P. Petitgas [eds.], Manual of recommended practices for modelling physical-biological interactions during fish early life. ICES Cooperative Research Report No. 295.

Laughton, R. 1991. The movements of adult Atlantic Salmon (*Salmo salar* L.) in the River Spey as Determined by Radio Telemetry During 1988 and 1989. Scottish Fisheries Research Report **No. 50**: 36pp.

Lebreton, L. C.-M., S. D. Greer and J. C. Borrero. 2012. Numerical modelling of floating debris in the world's oceans. Marine Pollution Bulletin **64**: 653–661.

Lett, C., P. Verley, C. Mullon, C. Parada, T. Brochier, P. Penven and B. Blanke. 2008. A Lagrangian tool for modelling ichthyoplankton dynamics. Environmental Modelling & Software **23**: 1210–1214.

Li, Y. and S. M. Çalişal. 2010. Numerical analysis of the characteristics of vertical axis tidal current turbines. Renewable Energy **35**: 435–442.

Liu, W.-C., W.-B. Chen and M.-H. Hsu. 2011. Using a three-dimensional particle-tracking model to estimate the residence time and age of water in a tidal estuary. Computers & Geosciences **37**: 1148–1161.

Lohmann, K. J. and C. M. F. Lohmann. 2006. Sea turtles, lobsters, and oceanic magnetic maps. Marine and Freshwater Behaviour and Physiology **39**: 49–64.

Lohmann, K. J., C. M. F. Lohmann and C. S. Endres. 2008. The sensory ecology of ocean navigation. The Journal of Experimental biology **211**: 1719–28.

Lohmann, K. J., N. F. Putman and C. M. Lohmann. 2011. The magnetic map of hatchling loggerhead sea turtles. Current Opinion in Neurobiology **22**: 336–342.

MacKenzie, K. M., C. N. Trueman, M. R. Palmer, A. Moore, A. T. Ibbotson, W. R. C. Beaumont and I. C. Davidson. 2012. Stable isotopes reveal age-dependent trophic level and spatial segregation during adult marine feeding in populations of salmon. ICES Journal of Marine Science **69**: 1637–1645.

Malcolm, I. A., J. Godfrey and A. F. Youngson. 2010. Review of migratory routes and behaviour of Atlantic salmon, Sea trout and European eel in Scotland's coastal environment: implications for the development of marine renewables. Scottish Marine and Freshwater Science. **Volume 1**: No 14. 82pp.

Mariani, P., B. R. MacKenzie, D. Iudicone and A. Bozec. 2010. Modelling retention and dispersion mechanisms of bluefin tuna eggs and larvae in the northwest Mediterranean Sea. Progress In Oceanography **86**: 45–58.

Masumoto, Y. 2010. Sharing the results of a high-resolution ocean general circulation model under a multi-discipline framework—a review of OFES activities. Ocean Dynamics **60**: 633–652.

McCormick, S. D., L. P. Hansen, T. P. Quinn and R. L. Saunders. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **55**: 77–92.

McCubbin, D., K. S. Leonard, J. Brown, P. J. Kershaw, R. A. Bonfield and T. Peak. 2002. Further studies of the distribution of technetium-99 and caesium-137 in UK and European coastal waters. Continental Shelf Research **22**: 1417–1445.

Menzies, W. J. M. 1937. The Movements of Salmon marked in the Sea. I. The North-west Coast of Scotland in 1936. Fishery Board for Scotland. Salmon Fisheries **Number 1**: 17pp.

Montgomery, J. C., A. Jeffs, S. D. Simpson, M. Meekan and C. Tindle. 2006. Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. Advances in Marine Biology **51**: 143–96.

Mork, K. A., J. Gilbey, L. P. Hansen, A. J. Jensen, J. A. Jacobsen, F. Vikebø, P. Mcginnity, M. Holm, J. C. Holst, O. Niall, W. Melle, K. Thomas, E. Verspoor and V. Wennevik. 2012. Modelling the migration of post-smolt Atlantic salmon (*Salmo salar*) in the Northeast Atlantic. ICES Journal of Marine Science **69**: 1616–1624.

Nall, H. G. 1930. The Life of the Sea Trout. Seeley Service & Co. London.

Narazaki, T., K. Sato, K. J. Abernathy, G. J. Marshall and N. Miyazaki. 2009. Sea turtles compensate deflection of heading at the sea surface during directional travel. The Journal of Experimental Biology **212**: 4019–26.

Nevitt, G. A., A. H. Dittman, T. P. Quinn and W. J. Moody. 1994. Evidence for a peripheral olfactory memory in imprinted salmon. Proceedings of the National Academy of Sciences of the United States of America **91**: 4288–92.

Nordeng, H. A. 1977. A pheromone hypothesis for homeward migration in anadromous salmonids. Oikos **28**: 155–159.

North, E. W., A. Gallego and P. Petitgas,eds. 2009. Manual of recommended practices for modelling physical – biological interactions during fish early life. ICES Cooperative Research Report No. 295.

Ogura, M. and Y. Ishida. 1995. Homing behavior and vertical movements of 4 species of pacific salmon (*Oncorhynchus* spp) in the central Bering sea. Canadian Journal of Fisheries and Aquatic Sciences **52**: 532–540.

Ohshima, K. I. and D. Simizu. 2008. Particle Tracking Experiments on a Model of the Okhotsk Sea: Toward Oil Spill Simulation. Journal of Oceanography **64**: 103–114.

Olbert, A. I., M. Hartnett and T. Dabrowski. 2010a. Assessment of Tc-99 monitoring within the western Irish Sea using a numerical model. Science of the Total Environment **408**: 3671–82.

Olbert, A. I., M. Hartnett, T. Dabrowski and K. Kelleher. 2010b. Effects of complex hydrodynamic processes on the horizontal and vertical distribution of Tc-99 in the Irish Sea. Science of the Total Environment **409**: 150–61.

van Opzeeland, I. and H. Slabbekoorn. 2012. Importance of underwater sounds for migration of fish and aquatic mammals, p. 357–359. *In* A.N. Popper and A. Hawkins [eds.], The Effects of Noise on Aquatic Life. Springer. New York, NY.

Orre, S., Y. Gao, H. Drange and E. Deleersnijder. 2008. Diagnosing Ocean Tracer Transport from Sellafield and Dounreay by Equivalent Diffusion and Age. Advances in Atmospheric Sciences **25**: 805–814.

Paris, C. B., R. K. Cowen, R. Claro and K. C. Lindeman. 2005. Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. **296**: 93–106.

Periáñez, R. and A. Pascual-Granged. 2008. Modelling surface radioactive, chemical and oil spills in the Strait of Gibraltar. Computers & Geosciences **34**: 163–180.

Perry, R. W., J. M. Plumb, S. D. Fielding, N. S. Adams and D. W. Rondorf. 2013. Comparing Effects of Transmitters within and among Populations: Application to Swimming Performance of Juvenile Chinook Salmon. Transactions of the American Fisheries Society **142**: 901–911.

Plew, D. R. and C. L. Stevens. 2013. Numerical modelling of the effect of turbines on currents in a tidal channel – Tory Channel, New Zealand. Renewable Energy **57**: 269–282.

Popper, A. N. and C. R. Schilt. 2008. Hearing and Acoustic Behavior: Basic and Applied Considerations, p. 17–48. *In* J.F. Webb, R.R. Fay, and A.N. Popper [eds.], Fish Bioacoustics: Springer Handbook of Auditory Research Volume 32. Springer Science. New York, NY.

Potter, E. C. E. and A. Swain. 1982. Effects of the English North-East coast salmon fisheries on Scottish salmon catches. MAFF Directorate of Fisheries Research: Fisheries Research Technical Report **Number 67**: 8.

Pous, S., E. Feunteun and C. Ellien. 2010. Investigation of tropical eel spawning area in the South-Western Indian Ocean: Influence of the oceanic circulation. Progress In Oceanography **86**: 396–413.

Power, J. H. and J. D. McCleave. 1983. Simulation of the North Atlantic ocean drift of *Anguilla* leptocephali. Fishery Bulletin **81**: 483–500.

Pritchard, M. and D. A. Huntley. 2006. A simplified energy and mixing budget for a small river plume discharge. Journal of Geophysical Research **111**: C03019.

Putman, N. F., C. S. Endres, C. M. F. Lohmann and K. J. Lohmann. 2011. Longitude perception and bicoordinate magnetic maps in sea turtles. Current Biology **21**: 463–6.

Putman, N. F., K. J. Lohmann, E. M. Putman, T. P. Quinn, A. P. Klimley and D. L. G. Noakes. 2013. Evidence for Geomagnetic Imprinting as a Homing Mechanism in Pacific Salmon. Current Biology 1–5.

Putman, N. F., P. Verley, T. J. Shay and K. J. Lohmann. 2012. Simulating transoceanic migrations of young loggerhead sea turtles: merging magnetic navigation behavior with an ocean circulation model. Journal of Experimental Biology **215**: 1863–1870.

Qiu, Z., A. M. Doglioli, Y. He and F. Carlotti. 2011. Lagrangian model of zooplankton dispersion: numerical schemes comparisons and parameter sensitivity tests. Chinese Journal of Oceanology and Limnology **29**: 438–445.

Quinn, T. P. 1980. Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. Journal Of Comparative Physiology **137**: 243–248.

Quinn, T. P. 2005. The Behaviour and Ecology of Pacific Salmon and Trout. University of Washington Press. Seattle.

Quinn, T. P. and E. L. Brannon. 1982. The use of celestial and magnetic cues by orienting sockeye salmon smolts. Canadian Journal Of Zoology **147**: 547–552.

Quinn, T. P., R. T. Merrill and E. L. Brannon. 1981. Magnetic field detection in sockeye salmon. Journal of Experimental Zoology **217**: 137–142.

Quinn, T. P., I. J. Stewart and C. P. Boatright. 2006. Experimental evidence of homing to site of incubation by mature sockeye salmon, *Oncorhynchus nerka*. Animal Behaviour **72**: 941–949.

Quinn, T. P., B. A. Terhart and C. Groot. 1989. Migratory Orientation and Vertical Movements of Homing Adult Sockeye Salmon, *Oncorhynchus nerka*, in Coastal Waters. Animal Behaviour **37**: 587–599.

Radford, A., G. Riddington, J. Anderson and H. Gibson. 2004. The Economic Impact of Game and Coarse Angling in Scotland. Scottish Executive. Edinburgh.

Radford, C. A., A. G. Jeffs, C. T. Tindle and J. C. Montgomery. 2008. Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. Oecologia **156**: 921–9.

Reddin, D. G., L. P. Hansen, V. Bakkestuen, I. Russell, J. White, E. C. E. Potter, J. B. Dempson, T. F. Sheehan, N. O'Maoileidigh, G. W. Smith, A. Isaksson, J. A. Jacobsen, M. Fowler, K. A. Mork and P. Amiro. 2012. Distribution and biological characterstics of Atlantic salmon (*Salmo salar*) at Greenland based on the analysis of historical tag recoveries. ICES Journal of Marine Science **69**: 1589–1597.

Ritz, T., R. Wiltschko, P. J. Hore, C. T. Rodgers, K. Stapput, P. Thalau, C. R. Timmel and W. Wiltschko. 2009. Magnetic compass of birds is based on a molecule with optimal directional sensitivity. Biophysical Journal **96**: 3451–7.

Russon, I. J. and P. S. Kemp. 2011. Advancing provision of multi-species fish passage: Behaviour of adult European eel (*Anguilla anguilla*) and brown trout (*Salmo trutta*) in response to accelerating flow. Ecological Engineering **37**: 2018–2024.

SALSEA-MERGE. 2012. Project final report. http://www.nasco.int/sas/pdf/salsea_documents/salsea_merge_finalreports/Completed%20Final%20Report%20SALSEA-Merge.pdf.

Sand, O., P. S. Enger, H. E. Karlsen and F. R. Knudsen. 2001. Detection of infrasound in fish and behavioral responses to intense infrasound in juvenile salmonids and European silver eels: A minireview. American Fisheries Society Symposium **26**: 183–193.

Sand, O. and H. E. Karlsen. 2000. Detection of infrasound and linear acceleration in fishes. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **355**: 1295–1298.

Satterthwaite, W. H., M. S. Mohr, M. R. O'Farrell and B. K. Wells. 2013. A comparison of temporal patterns in the ocean spatial distribution of California's Central Valley Chinook salmon runs. Canadian Journal of Fisheries and Aquatic Sciences 1–42.

Scholz, A. T., R. M. Horrall, J. C. Cooper and A. D. Hasler. 1976. Imprinting to chemical cues: the basis for home stream selection in salmon. Science **192**: 1247–1249.

Scott, R., R. Marsh and G. C. Hays. 2012. A little movement orientated to the geomagnetic field makes a big difference in strong flows. Marine Biology **159**: 481–488.

Scottish Government. 2012. 2020 Renewable Routemap for Scotland - Update. http://www.scotland.gov.uk/Resource/0040/00406958.pdf. 49pp.

Shelton, R. G. J., W. R. Turrell, A. MAcdonald, I. S. McLaren and N. T. Nicoll. 1997. Records of post-smolt Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. Fisheries Research **31**: 159–162.

Simons, A. M. 2004. Many wrongs: the advantage of group navigation. Trends in Ecology & Evolution **19**: 453–5.

Simons, R. D., D. A. Siegel and K. S. Brown. 2013. Model Sensitivity and Robustness in the Estimation of Larval Transport: A Study of Particle Tracking Parameters. Journal of Marine Systems **119-120**: 19–29.

Slabbekoorn, H. and N. Bouton. 2008. Soundscape orientation: a new field in need of sound investigation. Animal Behaviour **76**: e5–e8.

Smith, G. W., A. D. Hawkins, G. G. Urquhart and W. M. Shearer. 1979. Orientation and Energetic Efficiency in the Offshore Movements of Returning Atlantic Salmon *Salmo salar* L . Scottish Fisheries Research Report 22.

Smith, L. S. 1982. Decreased swimming performance as a necessary component of the smolt migration in salmon in the Columbia River. Aquaculture **28**: 153–161.

Soomere, T., O. Andrejev, K. Myrberg and A. Sokolov. 2011. The use of Lagrangian trajectories for the identification of the environmentally safe fairways. Marine Pollution Bulletin **62**: 1410–20.

Stapput, K., O. Güntürkün, K.-P. Hoffmann, R. Wiltschko and W. Wiltschko. 2010. Magnetoreception of directional information in birds requires nondegraded vision. Current Biology **20**: 1259–62.

Stewart, D. C., G. W. Smith and A. F. Youngson. 2002. Tributary-specific variation in timing of return of adult Atlantic salmon (*Salmo salar*) to fresh water has a genetic component. **281**: 276–281.

Symonds, A. M. 2011. A comparison between far-field and near-field dispersion modelling of fish farm particulate wastes. Aquaculture Research **42**: 73–85.

Tanaka, H., Y. Naito, N. Davis, S. Urawa, H. Ueda and M. Fukuwaka. 2005. First record of the at-sea swimming speed of a Pacific salmon during its oceanic migration. Marine Ecology Progress Series **291**: 307–312.

Taylor, P. B. 1986. Experimental evidence for geomagnetic orientation in juvenile salmon, *Oncorhynchus tschawytscha* Walbaum. Journal of Fish Biology **28**: 607–623.

Thomsen, F., K. Luedemann, W. Piper, A. Judd and R. Kafemann. 2008. Potential effects of offshore wind farm noise on fish. Bioacoustics **17**: 221–223.

Thorstad, E. B., F. Whoriskey, I. Uglem, A. Moore, A. H. Rikardsen and B. Finstad. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. Journal of Fish Biology **81**: 500–42.

Thorup, K., R. A. Holland, A. P. Tøttrup and M. Wikelski. 2010. Understanding the migratory orientation program of birds: extending laboratory studies to study free-flying migrants in a natural setting. Integrative and Comparative Biology **50**: 315–22.

Thygesen, U. H. 2011. How to reverse time in stochastic particle tracking models. Journal of Marine Systems **88**: 159–168.

Tian, R. C., C. Chen, K. D. E. Stokesbury, B. J. Rothschild, G. W. Cowles, Q. Xu, S. Hu, B. P. Harris and M. C. I. Marino. 2009. Dispersal and settlement of sea scallop larvae spawned in the fishery closed areas on Georges Bank. ICES Journal of Marine Science **66**: 2155–2164.

Turrell, W. R. 1992. New hypotheses concerning the circulation of the northern North Sea and its relation to North Sea fish stock recruitment. ICES Journal of Marine Science **49**: 107–123.

Turrell, W. R., E. W. Henderson and G. Slesser. 1990. Residual transport within the Fair Isle Current observed during the Autumn Circulation Experiment (ACE). Continental Shelf Research **10**: 521–543.

Turrell, W. R., G. Slesser, R. Payne, R. D. Adams and P. A. Gillibrand. 1996. Hydrography of the East Shetland Basin in relation to decadal North Sea variability. ICES Journal of Marine Science **53**: 899–916.

UKMMAS. 2010. Charting Progress 2 Feeder Report: Ocean Processes (Ed. Huthnance, J). Produced by Department for Environment Food and Rural Affairs on behalf of the United Kingdom Marine Monitoring and Assessment Strategy. http://chartingprogress.defra.gov.uk/ocean-processes-feeder-report. 279 pp.

Verspoor, E., S. Consuegra, O. Fridjonsson, S. Hjorleifsdottir, D. Knox, K. Olafsson, S. Tompsett, V. Wennevik and C. Garcia de Leaniz. 2012. Regional mtDNA SNP differentiation in European Atlantic salmon (*Salmo salar*): an assessment of potential utility for determination of natal origin. ICES Journal of Marine Science **69**: 1625–1636.

Vickers, N. J. 2000. Mechanisms of animal navigation in odor plumes. The Biological Bulletin **198**: 203–12.

Villaret, C., J. M. Hervouet, N. Huybrechts, L. A. Van and A. G. Davies. 2009. Effect of bed friction on morphodynamic modelling: Application to the central part of the Gironde estuary. River, Coastal and Estuarine Morphodynamics 899–906.

Visser, A. W. 1997. Using random walk models to simulate the vertical distribution of particles in a turbulent water column. Marine Ecology Progress Series **158**: 275–281.

Vogel, S. 1994. Life in moving fluids: The physical biology of flow. 2nd Edition. Princeton University Press. Princeton, New Jersey.

Vøllestad, L. A., D. Hirst, J. H. L'Abée-Lund, J. D. Armstrong, J. C. MacLean, A. F. Youngson and N. C. Stenseth. 2009. Divergent trends in anadromous salmonid populations in Norwegian and Scottish rivers. Proceedings of the Royal Society B-Biological Sciences **276**: 1021–1027.

Wahlberg, M. and H. Westerberg. 2005. Hearing in fish and their reactions to sounds from offshore wind farms. Marine Ecology Progress Series **288**: 295–309.

Walker, M. M. and T. E. Dennis. 2005. Role of the magnetic sense in the distribution and abundance of marine animals. Marine Ecology Progress Series **287**: 295–300.

Walker, M. M., C. E. Diebel, C. V Haugh, P. M. Pankhurst, J. C. Montgomery and C. R. Green. 1997. Structure and function of the vertebrate magnetic sense. Nature **390**: 371–6.

Walter, E. E., J. P. Scandol and M. C. Healey. 1997. A reappraisal of the ocean migration patterns of Fraser River sockeye salmon (*Oncorhynchus nerka*) by individual-based modelling. Canadian Journal of Fisheries and Aquatic Sciences **54**: 847–858.

Went, A. E. J. 1973. Movements of salmon *Salmo salar* (L.) to and from Irish waters. Journal of Fish Biology **5**: 659–671.

Went, A. E. J. 1976. The recapture of British salmon in Irish waters. Journal of Fish Biology **8**: 311–316.

Wenz, G. M. 1962. Acoustic ambient noise in the ocean: spectra and sources. Journal of the Acoustical Society of America **34**: 1936–1957.

Willis, J. 2011. Modelling swimming aquatic animals in hydrodynamic models. Ecological Modelling **222**: 3869–3887.

Willis, J., J. Phillips, R. Muheim, F. J. Diego-Rasilla and A. J. Hobday. 2009. Spike dives of juvenile southern bluefin tuna (*Thunnus maccoyii*): a navigational role? Behavioral Ecology and Sociobiology **64**: 57–68.

Wiltschko, W. and R. Wiltschko. 1991. Magnetic orientation and celestial cues in migratory orientation., p. 16–37. *In* P. Berthold [ed.], Orientation in Birds. Birkhauser Science. Basel.

Wiltschko, W. and R. Wiltschko. 2012. Global navigation in migratory birds: tracks, strategies, and interactions between mechanisms. Current Opinion in Neurobiology **22**: 328–35.

Winther, N. G. and J. A. Johannessen. 2006. North Sea circulation: Atlantic inflow and its destination. Journal of Geophysical Research **111**: C12018.

Wiseman, W. J. and R. W. Garvine. 1995. Plumes and Coastal Currents Near Large River Mouths. Estuaries **18**: 509–517.

WWF. 2001. The Status of Wild Atlantic Salmon: A River by River Assessment. http://wwf.panda.org/about_our_earth/blue_planet/publications/?3729/TheStatus-of-Wild-Atlantic-Salmon-A-River-by-River-Assessment. 184 pp.

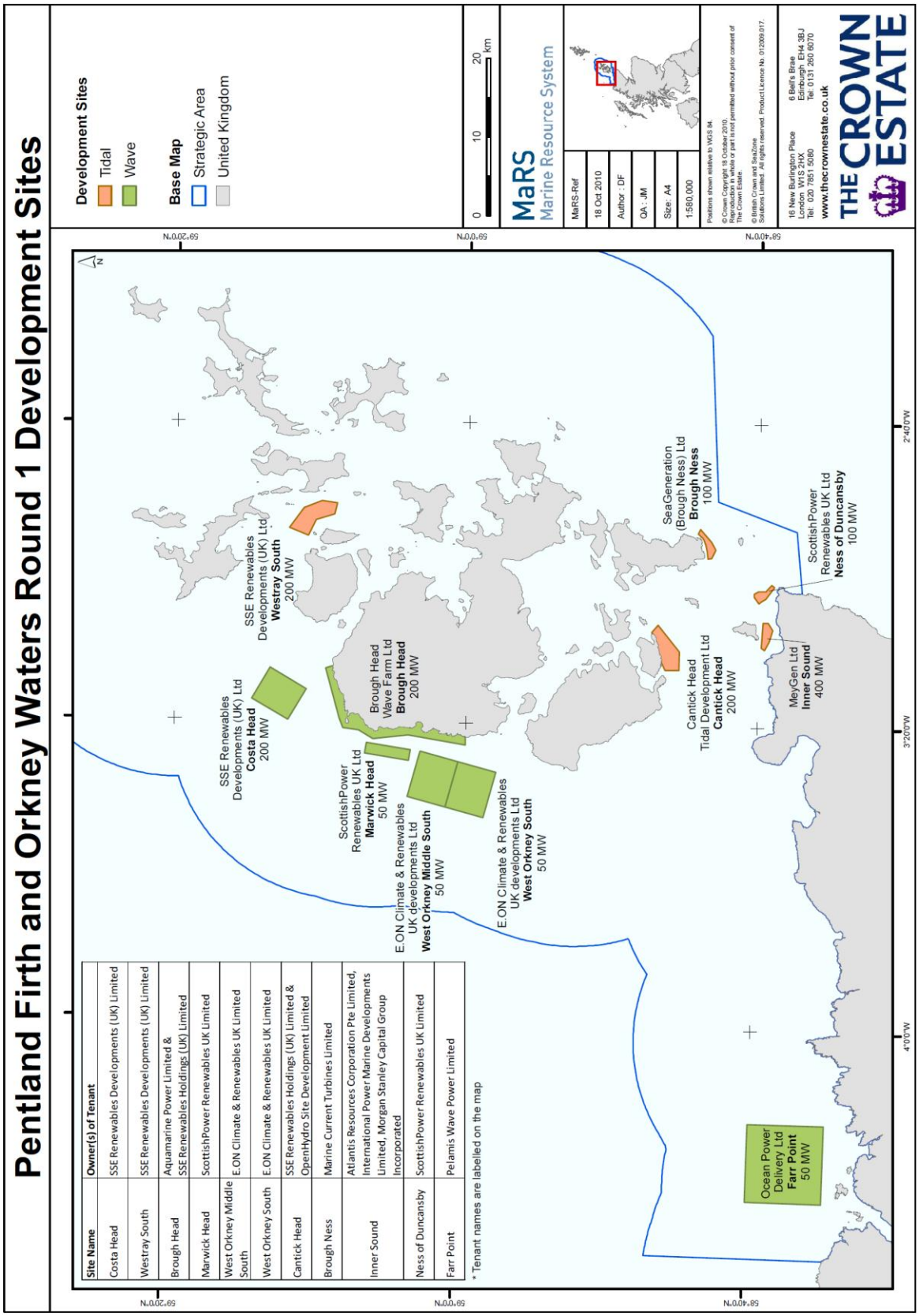
Yoon, J.-H., S. Kawano and S. Igawa. 2010. Modeling of marine litter drift and beaching in the Japan Sea. Marine Pollution Bulletin **60**: 448–63.

Youngson, A. F., W. C. Jordan and D. W. Hay. 1994. Homing of Atlantic Salmon (*Salmo salar* L.) to a Tributary Spawning Stream in a Major River Catchment. Aquaculture **121**: 259–267.

Youngson, A. F., J. C. MacLean and R. J. Fryer. 2002. Rod catch trends for early-running MSW salmon in Scottish rivers (1952–1997): divergence among stock components. ICES Journal of Marine Science **59**: 836–849.

Zenimoto, K., Y. Sasai, H. Sasaki and S. Kimura. 2011. Estimation of larval duration in *Anguilla* spp., based on cohort analysis, otolith microstructure, and Lagrangian simulations. Marine Ecology Progress Series **438**: 219–228.

Appendix – Crown Estate Tidal and Wave leasing sites - Pentland Firth and Orkney Waters



The Crown Estate
16 New Burlington Place
London W1S 2HX
Tel: 020 7851 5080

6 Bell's Brae
Edinburgh EH4 3BJ
0131 230 6070

www.thecrownestate.co.uk

ISBN: 978-1-906410-52-0